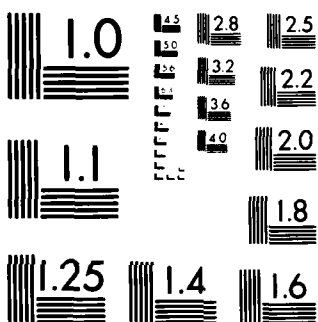


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**A deep-sea benthic community exposed to strong
near-bottom currents on the Scotian rise
(Western Atlantic)**

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Key Words: deep sea, benthos, animal-flow interactions

running head: the benthic community

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ABSTRACT

This paper gives an overview of the structure of a benthic community at 4626 m depth on the Nova Scotian continental rise. Here, abundances of polychaetes, bivalves, isopods, and tanaids are conspicuously high compared to those reported from comparable depths. Bacterial numbers and ATP concentrations are also high. We suspect that these anomalous abundances result from enhanced food abundance caused by the strong near-bottom currents that flow through the area. The polychaete and bivalve faunas have few adults and high species dominance suggesting that currents create large-scale, sediment-transporting disturbances. The composition of the crustacean fauna supports this inference in that it is dominated by forms that can enter the seabed and thereby escape adverse conditions on the sediment surface.

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INTRODUCTION

Investigation of the deep-sea benthos began in the 1800's (Mills, 1983). Yet, because of the vastness of the realm and the difficulty of obtaining information about the organisms living there, deep-sea communities are far from fully described. Much of our knowledge comes from regions with quiescent hydrodynamic conditions, and, as a result, the deep sea has been characterized as a physically stable environment (Sanders, 1968). It is now being recognized that the deep sea is not always or everywhere quiescent (Heezen and Hollister, 1964; Rowe and Menzies, 1968; Dinet and Vivier, 1977; Gage, 1979; Rowe, 1981). Vast areas have bedforms that appear to have been created by strong near-bottom flows (Hollister and Heezen, 1972). The community described in this paper occurs in a hydrodynamically active area on the Nova Scotian rise, where strong near-bottom currents (Richardson, Wimbush and Mayer, 1981) episodically erode the surface of the sea bed (Yingst and Aller, 1982; McCave et al., submitted). The description of this community is of interest because it experiences conditions that differ from those of the more familiar, physically stable deep-sea areas, and because it may be representative of communities beneath strong deep-sea currents worldwide. In this paper, we contrast a benthic community on the Scotian Rise with other deep-sea communities and attempt to understand the differences in terms of the impact of the near-bottom flow regime.

The samples upon which our description is based were taken as part of the High Energy Benthic Boundary Layer Experiment (HEBBLE) (Nowell, Hollister, and Jumars, 1982). This project is an interdisciplinary study of sediment transport in the deep ocean where near-bottom current

velocities are intermittently high. Because sediment-transport parameters in many environments are significantly altered by the organisms living in the sediment (Rhoads, 1974; Young and Southard, 1978; Nowell, Jumars, and Eckman, 1981; Rhoads and Boyer, 1982), biological studies are an important component of the project.

LOCALITY

The study site is on the Nova Scotian rise at 4626 m depth (Figure 1). In this region, currents alter sea-bed topography (Hollister and Heezen, 1972). A nine-month current-meter record taken nearby (33 km away at 4500 m depth) documents frequent, several-day-long periods when daily-averaged, current velocities at 10 m above bottom were 20-25 cm/sec (Weatherly and Kelley, 1983). These velocities are conspicuously higher than the 3 cm/sec typical of abyssal conditions (Munk, Snodgrass, and Wimbush, 1970) and are among the highest ever measured in the deep sea (Richardson et al., 1981). These "benthic storms" (Kerr, 1980) erode surficial sediment (Weatherly and Kelley, 1983), producing near-bottom suspended particulate matter concentrations that are at times much greater than those of strong nepheloid layers known elsewhere in the world ocean, for example, 0.78 parts per million volume concentration of suspended matter versus 0.03 ppm in clear sea water (Weatherly and Kelly, 1983). These periods of rapid erosion appear to alternate with periods of massive deposition (Yingst and Aller, 1982).

Two locations 3 km apart but at the same depth were sampled: Knorr 78 Station 7 (40°24.0'N, 63°07.4'W) and Knorr 78 Station 14 (40°24.3'N, 63°09.6'W). In this region, near-bottom temperature varies between 2.23°C and 2.27°C and the salinity varies between 34.85‰ and 34.9‰ (Weatherly, pers. commun., 1982). Disaggregated-grain-size analyses show the sediments to be composed of 6.0% sand, 50.6% silt, and 39.3% clay on the average (Tucholke, unpublished data). The clay- and silt-sized particles are incorporated in and mixed with particle aggregates > 500 μ m

including fecal pellets, arenaceous and calcareous foraminiferan tests, and glacially rafted pebbles (Yingst and Aller, 1982; Thistle, 1983a). The sediment is consolidated compared to shallow-water deposits of similar composition (Yingst and Aller, 1982) and is oxidized to at least 10 cm depth. X-radiographs of vertical sediment slabs reveal physically produced sediment layers, abundant tubes and burrows, and localized areas homogenized by biological reworking (Yingst and Aller, 1982) (Figure 2). Organic-carbon and organic-nitrogen concentrations are higher throughout the top 10 cm than in many deep-sea regions and the C/N ratio suggests that the surficial organic matter can be further metabolized (Yingst and Aller, 1982; Yingst, in preparation).

Thistle (1983b) refers to this location as the HEBBLE site. It is not. The HEBBLE site is at 4820 m depth (40° 27'N 62° 20'W) about 68.6 km away from the location of these preliminary samples.

MATERIALS AND METHODS

The samples were taken from R/V Knorr (cruise 78) using a $1/4 \text{ m}^2$ box corer (Hessler and Jumars, 1974) equipped with the modifications originated by R.R. Hessler, P.A. Jumars and J. Finger to reduce bow wave (see Thistle, 1983b, for more description). The box corer box contained removable subsamplers (Figure 3). The central nine $10 \text{ cm} \times 10 \text{ cm}$ subcores contained $5 \text{ cm} \times 5 \text{ cm}$ subsubcores whose bottom edges were beveled such that they sampled 23 cm^2 . Sediment slabs for x-radiography were taken from the 10 cm by 30 cm region (Figure 3).

Faunal samples (77 cm^2) were processed as follows. At sea, the water overlying a subcore was drawn off and passed through a 0.045-mm sieve, and the residue added to the $0\text{-}1 \text{ cm}$ layer sample. The sediment was then extruded and sliced into the following layers: $0\text{-}1$, $1\text{-}2$, $2\text{-}3$, $3\text{-}5$, $5\text{-}7$, and $7\text{-}10 \text{ cm}$. Samples were preserved in buffered 20% formaldehyde-filtered seawater. In the laboratory, each layer was washed on sieves with the following apertures: 1.00 , 0.500 , 0.420 , 0.297 , and 0.063 mm . The $\geq 0.297 \text{ mm}$ fractions were rose bengal stained and sorted under a dissecting microscope. The animals in the 0.063-mm fraction were concentrated using the Barnett (1968) procedure (efficiency was 100% for harpacticoids and 99.7% for nematodes (median of 3 trials)), rose bengal stained, and sorted under a dissecting microscope. Nematodes were counted; other taxa were picked. Values reported for nematodes and harpacticoids include individuals found in all fractions; values reported for macrofauna include only individuals from the $\geq 0.297\text{-mm}$ fractions. The $0\text{-}5 \text{ cm}$ layers were enumerated for macrofauna. For nematodes and harpacticoids, the $0\text{-}2 \text{ cm}$ layer data reported account for the bulk of the fauna. For example, the $2\text{-}3 \text{ cm}$ layer adds a median of 14.8% more nematodes ($N=18$) (Thistle and Sherman, in preparation).

Bacteria were counted directly from glutaraldehyde-preserved subsamples (0.3% glutaraldehyde in 3% NaCl) using the epifluorescence method of Hobbie et al. (1977) as modified by Watson et al. (1977) (see Aller and Yingst, 1980, for details). Sediment adenosine triphosphate (ATP) concentrations were determined aboard ship as soon after sample collection as possible, usually < 4 h, using either the boiling sodium bicarbonate method of Christian et al. (1975) or the boiling phosphate buffer method (Bulleid, 1978). All samples were extracted in duplicate and ATP concentrations calculated using standard curves determined with sediment from this area prepared to be axenic and essentially ATP-free. These curves are designed to correct for interference in the luciferin-luciferase assay caused by chemical characteristics of the sediment that are proportional to the weight of sediment extracted (Yingst, in preparation).

In our among-site comparison, we have considered each major taxon separately for the taxa that were abundant in our samples. Literature reports and our own data are expressed as the number per $1/4 \text{ m}^2$ for macrofauna, number per 10 cm^2 for nematodes and harpacticoids, and number per g of sediment for bacteria for each box core. Benthic copepod and harpacticoid copepod abundances are considered to be equivalent because harpacticoids overwhelmingly dominate the benthic copepod assemblage. We tested the abundance of each macrofaunal taxon against Khripounoff, Desbruyères, and Chardy's (1980) results because, of the studies where replicate box cores were taken at a site, their site at 5100 m in the Vema Fracture Zone (station B) most nearly approximates the depth at our site.

RESULTS AND DISCUSSION

Abundance and Composition of Major Taxa

Although deep-sea communities have been sampled since the 1800's, quantitative estimates of infaunal standing stocks have been made only since the advent of box-coring techniques in the 1970's. Quantitative samples using sampling methods comparable to those we used have been taken in only a small number of sites (Table 1). We use these data to compare with our results.

Table 2 gives the composition of the fauna at our site. The taxa listed are among those commonly found in the deep sea. Our list is shorter than most because some rare taxa that have been collected by other investigators were not found. As is typical in the deep sea (Kripounoff et al., 1980, Table 5), polychaetes are the most abundant macrofaunal group and nematodes are the most abundant metazoan meiofaunal group.

Polychaetes are conspicuously more abundant at our site than at all but one other site from greater than 3000 m (Figure 4). In particular, their abundance is 6 times greater than the abundance found at a 4700-m site in the Bay of Biscay (Laubier and Sibuet, 1979) and is significantly greater than that found by Kripounoff et al. (1980).

The polychaete fauna resembles that of the other areas in the deep, northwest Atlantic in that the Paraonidae and Spionidae are important families (Hartman, 1965) (Table 3). However, the fauna differs from that found in other deep-sea locales in several ways. Cirratulidae is not among the dominant families (see stations II2, LL1, JJ1 in Hartman, 1965; Hessler and Jumars, 1974), but Ampharetidae is. The polychaete fauna of other deep-sea sites typically lacks strong dominance at the

species level (e.g., Hessler and Jumars, 1974), whereas, at our site, two undescribed species of Ampharetidae make up 58% and 64% of the polychaetes at stations 7 and 14 respectively. These ampharetids are small (1.5 -3.0 mm body length), as are many of the paraonids and spionids. Further, all of the polychaetes collected were sexually immature.

Although little direct evidence is available to assess the natural history of deep-sea polychaetes, analogies with shallow-water relatives suggest that our fauna is dominated by surface deposit feeders (Ampharetidae, Spionidae, Flabelligeridae, Cirratulidae and perhaps the single Sabellidae individual) (Jumars and Fauchald, 1977; Fauchald and Jumars, 1979) (Table 3). This dominance by surface deposit feeders agrees with data from other deep-sea areas (Hessler and Jumars, 1974; Jumars and Hessler, 1976; Gage, 1977). The Paraonidae and Cossuridae are subsurface deposit feeders. The members of the Hesionidae and Dorvilleidae and the species of Pilargiidae found in our samples appear to be carnivores. Most of the polychaete species we found belong to families known to be motile or discretely motile; the ampharetids are probably discretely motile despite their tubicolous habit (e.g., Amphicteis scaphobranchiata cf. Nowell, Jumars, and Fauchald, 1984).

The abundance of bivalves at our site is greater than that at all but one other site from deeper than 3000 m (Figure 5). Laubier and Sibuet's (1979) sample from the Bay of Biscay is most nearly from the same depth (4700 m); our value is more than 4 times greater and is significantly greater than that found by Khripounoff et al. (1980).

The bivalves are small in comparison to individuals of the same families and genera collected from similar depths elsewhere (G.R.

Hampson and H.L. Sanders, pers. commun., 1982). In addition, no sexually mature individuals were found. These circumstances contrast strongly with those reported by Grassle and Sanders (1973). The majority of the bivalves are protobranchs, e.g., Malletia abyssorum; 25% belong to the eulamellibranch family Thyasiridae, e.g., Thyasira subovata. Both groups are mobile surface and subsurface deposit feeders and are probably responsible for most of the localized areas of homogenized sediment seen in the x-radiographs where physically produced laminations and biologically produced burrows and tubes have been obliterated (Figure 2).

The abundance of isopods at our site is conspicuously greater than that at sites from similar depths (Figure 6). The median abundance is seven times greater than that found by Laubier and Sibuet (1979) at 4700 m, and the density of isopods is significantly greater than that at Kripounoff et al.'s (1980) 5100 m site. In fact, only Gage's (1979) sites in ≤ 2000 m depth in Rockall Trough have comparable densities. The isopods we found (Table 4) belong to typical deep-sea families (Hessler and Thistle, 1975), but only six of the 18 deep-sea janiroidean isopod families (Hessler and Wilson, 1983) are represented.

Nannoniscidae is the most abundant isopod family at our site. The species found have a long, thin body that seems more suitable for burrowing than does the broader body characteristic of other species of the family (J.F. Siebenaller, pers. commun., 1982). Ischnomesidae is second in abundance. These isopods have elongate bodies and long walking legs and are reminiscent of the walking-stick insects. Their habits are not well known. Wolff (1976) found specimens in seagrass rhizomes (see also George and Higgins, 1979); Gooday (submitted) found individuals in tube-like foraminiferan tests. We have found individuals

in the 1-2, 2-3, and 3-5 cm layers at the HEBBLE site. These observations suggest that ischnomesids are capable of burrowing or tube dwelling. Species of the other abundant isopod family, the Macrostylidae, have morphologies that suggest a tube- or burrow-dwelling life style. In sum, at our site the surface-living isopods seem to be rare, while those that can enter the sediment are unusually abundant in both relative and absolute terms.

The median abundance of tanaids at our site is higher than any value reported from the studies in Table 1 regardless of depth (Figure 7). It is more than an order of magnitude greater than Laubier and Sibuet's (1979) 4700-m value and significantly greater than that of Khrípounoff et al. (1980) from 5100 m. All of the tanaids we found belong to the suborder Dikonophora, and the majority belong to typically deep-sea families, the Paratanaidae and Leptognathiidae (Table 5) (Sars, 1896; Hansen, 1913; Nierstrasz, 1913; Lang, 1968). Many Paratanaidae and Leptognathiidae species construct tubes (Nierstrasz and Schuurmans Stekhoven Jr., 1930; Grieve, 1967). Although none of our specimens were found inside tubes, the morphology of the Leptognathiidae especially, with its short, stout legs, suggests a tube-dwelling habit (Johnson and Athramadal, 1982). Also, individuals of the surface dwelling family Neotanaidae are absent from our samples although they are common in other areas of the deep, northwest Atlantic (Gardiner, 1975). The tanaids, too, appear to be dominated by species that can enter the sediment.

Our values for nematode (Figure 8) and copepod densities (Figure 9) fall among reports from similar depths. However, this result should not be taken to imply that the composition of the meiofauna is typical for its depth. In particular, Thistle (1983b) has shown that the

harpacticoid fauna is depleted of surface-living species and is enriched in burrowing species.

There are few estimates based on direct-counting procedures of bacterial standing stocks in sediments with which to compare our results, but in general, bacterial standing stocks appear to decrease with increasing water depth (Yingst, in preparation). In contrast, our densities appear to be unusually high (Table 6). For example, they are comparable to those found at DOS II in 3480 m in the western Atlantic (Yingst, unpublished data), at stations in 100 to 230 m of water in the vicinity of the Texas Flower Garden Banks in the Gulf of Mexico (Yingst and Rhoads, in press), and at the Deep station in 40 m of water in Long Island Sound (Aller and Yingst, 1980). Sediment ATP concentrations similarly indicate high bacterial standing stocks in that they are approximately 8 times greater than those found at 6011 m on the Nares Abyssal Plain (Karl et al., 1976) and twice as great as Romano and Dinet (1978) found at 4010 and 4727 m in the northwestern Indian Ocean.

Interpretation of the Composition Data

In the deep sea, polychaetes and bivalves generally have been found to be relatively abundant and highly diverse (Sanders, Hessler, and Hampson, 1965; Sanders, 1968; Hessler and Jumars, 1974). By shallow-water standards, the distribution of individuals among species is even (i.e., low dominance) (e.g., Hessler, and Jumars, 1974), and large individuals (= adults) occur in and often dominate size-frequency tabulations (e.g., Grassle and Sanders, 1973). The polychaetes and bivalves from our site do not fit this pattern. Two polychaete species make up more than 50%

of the individuals; the polychaete and bivalve individuals are small pre-adults.

The only deep-sea studies that report faunas with these characteristics are those of Grassle (1977) and Desbruyères, Bervas, and Khripounoff (1980). Both papers report on recolonization studies at approximately 2000 m. Desbruyères et al. found when they recovered their experiment after 6 months that one species of polychaete made up 82% of the fauna. Also, they found only sub-adult bivalves and commented on the unusually high ratio of nauplii to adult harpacticoid copepods. Grassle found that Priapulus atlantisi dominated the fauna (30%) after 2 months and that most individuals of all taxa were sub-adults. These studies suggest that dominance by a small number of species and a preponderance of non-adults occurs in the deep sea when a defaunated patch is colonized primarily by larvae.

The similarity between our data and those of the recolonization experiments suggests that some factor at this locality is creating patches that are defaunated to some extent and are colonized by larvae from the water column. We know that locations in this region are subject to periods of intense erosion alternating with times of massive deposition, and such physical conditions can create defaunated patches (Eagle, 1975). Given that mesoscale oceanographic phenomena drive the system (Hollister, Nowell, and Jumars, 1984), it is likely that the patches produced will be large relative to the mobility of adult polychaetes and bivalves and that recolonization will be primarily by larvae (see Gerdes, 1977). So, as a working hypothesis, we suggest that our site is part of a region that has a patch structure

imposed on it in which defaunation is followed by larval recolonization.

The above scenario does not seem to fit the crustacean data. In particular, isopods and tanaids are unusually abundant in our samples. These peracarid crustaceans brood their young until they emerge as miniature adults. Lacking a planktonic stage, tanaids and isopods are thought to be poor dispersers. Why their numbers are high given the physical regime is unclear, but they do show the impact of the hydrodynamic conditions. That is, the only isopod groups abundant in our samples are those that can enter the sediment. The tanaids show the same pattern in that surface-living neotanaids are absent while burrow-dwelling families are extraordinarily abundant. Likewise, the harpacticoid copepod fauna has very few surface-living individuals (Thistle, 1983b). The ability of most of the crustacean species to enter the sea bed suggests that these species may be able to mitigate the effects of erosion and deposition at this site.

Interpretation of the Standing-Stock Data

Although some typically deep-sea taxa are absent or rare at our site, polychaetes, bivalves, isopods, and tanaids are much more abundant than in other deep-sea regions of comparable depth. The reason for the enhanced abundance is not clear, but it does not seem to be directly related to the productivity of the overlying water (see also Smith, Laver and Brown, 1983). In Table 7, we array the available data against productivity for each of the four taxa. The standing-stocks in our area remain anomalously high.

Although the high standing stocks could come about in a variety of ways, the hydrodynamic regime suggests two possibilities. Given that the mean current velocity at our site is greater than that of quiescent localities, even if the concentration of food in the overlying water is no greater, the flux of food available to animals that can extract suspended particulate food should be larger. For example, on our site a species of Oweniidae appears to be exploiting this food source. These tube-dwelling worms excavate pits around their tubes that passively extract particles from the near-bottom flow by decreasing the water velocity locally, causing material to fall from suspension (see Nowell, Jumars and Fauchald, 1984). Despite the apparently high flux of suspended food particles, ordinary suspension feeders (i.e., animals that use a mechanical filter) are not abundant. Work in shallow water has shown these organisms to be adversely affected by high suspended-sediment concentrations, which clog their filters (Rhoads and Young, 1970). The intermittently high suspended-matter concentrations on our site may exclude animals with this life style.

Second, recent work has shown that disruption of the microenvironment of sedimentary microbes stimulates their growth (Yingst and Rhoads, 1980; Allard, 1982). The erosion-deposition regime at our site appears to be capable of such disruption, so enhanced microbial production may explain a portion of the enhanced macrofaunal abundances. Further, the elevated bacterial numbers observed suggest that higher macrofaunal standing stocks can be maintained without reducing bacterial abundances to ordinary deep-sea levels, implying a decrease in the efficiency of

the coupling between these trophic levels that may be caused by the disturbance regime.

Given the large amount of suspended material observed, the currents at our site could bear enhanced concentrations of food that, in turn, could be supporting the high macrofauna numbers. For example, Gage (1979) speculates that the anomalously high biomass at 2000 m on the Feni Ridge (eastern North Atlantic) is related to a turbid bottom current having its origin in overflow water from the Norwegian Sea.

The circumstances related above suggest ways that the high standing stocks could occur, but before we conclude, we wish to point out a potential artifact of uncertain importance. The standing-stock comparison was based on numbers of individuals (as is typically done, see Thiel, 1983) rather than biomass because the latter data were not available. Given the preponderance of subadults among the HEBBLE polychaetes and bivalves (see above), the abundances of these two taxa could be inflated compared to sites where adults dominated the assemblage (assuming adult biomasses are comparable).

In conclusion, this site appears to contrast strongly with more familiar deep-sea soft-bottom habitats. In particular, macrofaunal standing stocks are unusually high and many species are adapted to shelter in the sediment. Both effects seem to be attributable to a hydrodynamic regime that is much more energetic than those in better studied areas of the deep ocean. Given that such energetic current regimes are not rare (Hollister, Nowell, and Jumars, 1984), present generalizations about the ecology of the deep sea may have to be modified.

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Table 1. Reports giving deep-sea faunal standing stocks that are comparable to our data. All studies used box corers but differed in details of sample handling including the sieve size used and the lowest depth to which the sediment was sampled. The abundances reported by Dinet et al. (1973) may be artifactually low according to Thiel (1983).

Author(s)	Region	Depth (m)	Sieve Aperture (mm)	Sample Depth (cm)
<u>Macrofauna</u>				
Hessler and Jumars (1974)	Central North Pacific	5634	0.297	0-20
Dahl, Laubier, Sibuet and Stromberg (1976)	Norwegian Sea	2479-3718	0.250	0-20
Jumars and Hessler (1976)	Aleutian Trench	7298	0.297	0-8
Gage (1977)	Rockall Trough	2875	0.420	core depth
Gage (1979)	Rockall Trough	1800-2900	0.420	≥ 25 cm
Laubier and Sibuet (1979)	Bay of Biscay	2000-4700	0.250	-
Khripounoff, Desbruyeres and Chardy (1980)	Vema Fracture Zone	5090-5880	0.250	core depth
<u>Meiofauna</u>				
Dinet (1973)	Walvis Ridge	1440-5170	0.040	0-3
Dinet, Laubier, Soyer and Vitiello (1973)	Mediterranean	2116-2855	0.050	0-4
Coull et al. (1977)	Western North Atlantic	400-4000	0.042	0-10
Dinet and Vivier (1977)	Bay of Biscay	1939-4645	0.050	0-4
Dinet (1979)	Norwegian Sea	2479-3709	0.040	0-5
George and Higgins (1979)	Puerto Rico Trench	8560-8580	0.062	0-7

Table 2. For macrofauna, total number of individuals in the 0-5 cm layers of nine 77 cm² subcores. For meiofauna, total number of individuals in the 0-2 cm layers of three 77 cm² subcores.

	Station	
	7	14
Macrofauna		
Polychaeta	111	75
Bivalvia	18	7
Aplacophora	1	0
Tanaidacea	9	34
Isopoda	18	24
Amphipoda	2	0
Cumacea	1	1
Sipunculida	5	0
Tardigrada	1	0
Total	166	141
Meiofauna		
Nematoda	4526	3297
Harpacticoida	313	192
Ostracoda	25	15
Kinorhyncha	22	11
Total	4886	3515

Table 3. The abundance by family of polychaetes found in the 0-5 cm layers.

Family	Station	
	7	14
Ampharetidae	64	48
Paraonidae	15	11
Spionidae	16	10
Cirratulidae	4	3
Hesionidae	4	0
Goniadidae	3	1
Cossuridae	1	0
Pilargiidae	1	0
Dorvilleidae	1	0
Sabellidae	1	0
Flabelligeridae	1	1
Phyllodoctidae	0	1
Unknown Family A	0	1
	<hr/>	<hr/>
Total	111	75

Table 4. The abundance by family of isopods found in the 0-5 cm layers.

Family	Station	
	7	14
Nannoniscidae	4	13
Ischnomesidae	3	6
Macrostylidae	5	0
Haploniscidae	1	2
Desmosomatidae	0	1
Pseudomesidae	0	2
(unidentifiable manca)	<u>5</u>	<u>0</u>
Total	18	24

Table 5. The abundance by family of tanaids found in the 0-5 cm layers.

Family	Station	
	7	14
Leptognathiidae	6	31
Pseudotanaidae	1	3
(unidentifiable damaged)	2	0
	<hr/>	<hr/>
	9	34

Table 6. Organic carbon, nitrogen, ATP concentrations and bacterial standing stocks (\pm S.D., N = 9) in discrete depth intervals at Stations 7 and 14.

Depth (cm)	ATP (ng/g)	(ng/cm ²)	Bacteria (10 ⁹ /g)	(10 ⁹ /cm ²)	Organic Carbon (mg/g)	Nitrogen (total) (mg/g)
Station 7						
0 - 1	12.93 \pm 3.2	8.39 \pm 2.08	18.26 \pm 6.85	11.85 \pm 4.45	5.70	0.52
1 - 2	10.5 \pm 1.95	6.98 \pm 1.3	12.23 \pm 4.24	8.13 \pm 2.82	5.20	0.55
2 - 3	8.05 \pm 0.66	5.60 \pm 0.44	10.86 \pm 2.53	7.56 \pm 1.76	4.80	0.47
3 - 5	7.23 \pm 0.79	5.23 \pm 0.57	9.74 \pm 2.39	7.05 \pm 1.73	4.30	0.47
5 - 7	6.8 \pm 1.2	5.48 \pm 0.97	7.52 \pm 1.26	6.06 \pm 1.02	3.90	0.62
7 - 10	5.02 \pm 1.73	3.29 \pm 1.13	6.61 \pm 1.18	4.34 \pm 0.77	4.00	0.65
Station 14						
0 - 1	10.57 \pm 1.17	7.28 \pm 0.81	21.6 \pm 7.05	14.88 \pm 4.86	6.07	0.68
1 - 2	9.28 \pm 1.6	8.57 \pm 1.48	15.12 \pm 4.42	13.97 \pm 4.08	5.52	0.77
2 - 3	7.83 \pm 0.33	6.55 \pm 0.28	17.37 \pm 4.26	14.54 \pm 3.57	4.96	0.69
3 - 5	8.38 \pm 0.97	7.74 \pm 0.87	15.41 \pm 2.52	14.48 \pm 2.33	4.08	0.65
5 - 7	7.71 \pm 0.61	8.29 \pm 0.66	12.20 \pm 2.27	13.12 \pm 2.44	3.80	0.65
7 - 10	6.87 \pm 0.51	4.70 \pm 0.35	9.89 \pm 1.20	6.76 \pm 0.82	3.17	0.52

Table 7. The abundance of the four macrofaunal taxa tabulated against water depth and levels of primary productivity in the overlying water. Relative productivity levels were taken from the version of Koblenz-Mishke, Volkoviskys^g and Kabanova's map in Gross (1982); Low=less than or equal to 100 mg C/m²/day, Moderate=100-250 mg C/m²/day, High=greater than 250 mg C/m²/day. The sources from which the abundances (per 1/4 m²) are taken are as follows: A=Hessler and Jumars, 1974; B=Gage, 1977; C=Gage, 1979; D=Laubier and Sibuet, 1979; E=Khripounoff, Desbruyères, and Chardy, 1980; F=our data. Dahl et al.'s (1976) data were omitted because of the difficulty of assessing ~~overlying-water~~ productivities in the Norwegian Sea.

		Depth (m)				
		1000-1999	2000-2999	3000-3999	4000-4999	5000-5999
A. Polychaetes						
Low						15 A
						17 E
						11 E
						3 E
Moderate		150 D	136 D		102 D	
		97 D			34 D	
		273 B			336 F	
		96 C				
		325 C				
High	414 C	224 C				
	185 C					

B. Bivalves

Low

2 A

8 E

2 E

2 E

Moderate

11 D

17 D

9 D

3 D

10 D

35 B

45 F

28 C

44 C

High

47 C

64 C

29 C

C. Isopods

Low

2 A

6 E

11 F

4 E

Moderate

13 D

11 D

1 D

18 D

11 D

20 B

76 F

23 C

131 C

High

107 C

19 C

24 C

D. Tanaids

Low

5 A

10 E

9 E

4 E

Moderate

23 D

19 D

10 D

30 D

5 D

42 B

78 F

32 C

77 C

High

50 C

26 C

26 C

References

- Aller, R.C., 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: P.L. McCall and M.J.S. Tevesz (Editors), *Animal-Sediment Relations*. Plenum, New York, pp. 53-102.
- Aller, R.C. and J.Y. Yingst, 1980. The relationship between bacterial distributions and anaerobic decomposition of organic matter in surface sediment of Long Island Sound, U.S.A. *Mar. Biol.*, 56: 29-42.
- Barnett, P.R.O., 1968. Distribution and ecology of harpacticoid copepods of an intertidal mud flat. *Int. Rev. Gesamten Hydrobiol.*, 53: 177-209.
- Bulleid, N.C., 1978. An improved method for the extraction of adenosine triphosphate from marine sediment and sea water. *Limnol. Oceanogr.*, 23: 174-178.
- Christian, R.R., K. Bancroft, and Wiebe, U.S., 1975. Distribution of microbial adenosine triphosphate in salt marsh sediments at Sapelo Island, Georgia. *Soil Sci.*, 119: 89-97.
- Coull, B.C., R.L. Ellison, J.W. Fleeger, R.P. Higgins, W.O. Hope, W.D. Hummon, R.M. Rieger, W.E. Sterrer, H. Thiel, and J.M. Tietjen, 1977. Quantitative estimates of the meiofauna from the deep sea off North Caroline, USA. *Mar. Biol.*, 39: 233-240.
- Dahl, E., L. Laubier, M. Sibuet and J.O. Stromberg, 1976. Some quantitative results on the benthic communities of the deep Norwegian Sea. *Astarte*, 9: 61-79.

- Desbruyères, D., J.Y. Bervas and A. Khripounoff, 1980. Un cas de colonisation rapide d'un sédiment profond. *Oceanologica Acta*, 3: 285-291.
- Dinet, A., 1973. Distribution quantitative du méiobenthos profond dans la région de la dorsale de Walvis (Sud-Ouest Africain), *Mar. Biol.*, 20: 20-26.
- Dinet, A., 1979. A quantitative survey of méiobenthos in the deep Norwegian Sea. *Ambio Special Report*, 6: 75-77.
- Dinet, A. and M.H. Vivier, 1977. Le méiobenthos abyssal du Golfe de Gascogne I. Considérations sur les données quantitatives. *Cah. Biol. Mar.*, 18: 85-97.
- Dinet, A., L. Laubier, J. Soyer et P. Vitiello, 1973. Resultats biologiques de la campagne Polymide II: le méiobenthos abyssal. *Rapp. Comm. Int. Mer. Medit.*, 21: 701-704.
- Eagle, R.A., 1975. Natural fluctuations in a soft bottom benthic community. *J. Mar. Biol. Assoc.*, 55: 865-878.
- Fauchald, K. and P.A. Jumars, 1979. The diet of worms; a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Annu. Rev.*, 17:193-284.
- Gage, J.D., 1977. Structure of the abyssal macrobenthic community in the Rockall Trough. In: B.F. Keegan, P. O'Ceidigh, and P.J.S. Boaden (Editors), *Biology of benthic organisms*. Pergamon Press, New York, pp. 247-260.
- Gage, J.D., 1979. Macrobenthic community structure in the Rockall Trough. *Ambio Special Report*, 6: 43-46.

- Gardiner, L.F., 1975. The systematics, postmarsupial development, and ecology of the deep-sea family Neotanaidae (Crustacea: Tanaidacea). *Smithson. Contrib. Zool.*, 170: 1-264.
- George, R.Y. and R.P. Higgins, 1979. Eutrophic hadal benthic community in the Puerto Rico Trench. *Ambio Special Report*, 6: 51-58.
- Gerdes, D., 1977. The re-establishment of an Amphiura filiformis (O.F. Muller) population in the inner part of the German Bight. In: B.F. Keegan, P. O'Ceidigh and P.J.S. Boaden (Editors), *Biology of benthic organisms*. Pergamon Press, New York, pp. 277-284.
- Gooday, A., submitted. Metazoans inhabiting the tests of deep-sea foraminifera and xenophyophora (Protozoa, Rhizopoda) in the northeast Atlantic.
- Grassle, J.F., 1977. Slow recolonization of deep-sea sediment. *Nature*, 265: 618-619.
- Grassle, J.F. and H.L. Sanders, 1973. Life histories and the role of disturbance. *Deep-Sea Res.*, 20: 643-659.
- Grieve, L., 1967. On the tube building of some Tanaidacea. *Sarsia*, 29: 295-298.
- Gross, M.G., 1982. *Oceanography*. Prentice-Hall, Englewood Cliffs, NJ, 498 pp.
- Hansen, H.J., 1913. Crustacea Malacostraca. II. IV, The Order Tanaidacea. Danish Ingolf-Expedition, 3(3): 1-145.
- Hartman, O., 1965. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Allan Hancock Foundation Occasional Publications*, 28: 1-378.
- Heezen, B.C. and C. Hollister, 1964. Deep-current evidence from abyssal sediments. *Mar. Geol.*, 1: 141-174.

- Hessler, R.R. and P.A. Jumars, 1974. Abyssal community analysis from replicate box cores in the central North Pacific. *Deep-Sea Res.*, 21: 185-209.
- Hessler, R.R. and D. Thistle, 1975. On the place of origin of the deep-sea isopods. *Mar. Biol.*, 32: 155-165.
- Hessler, R.R. and G.D.F. Wilson, 1983. The origin and biogeography of malacostracan crustaceans in the deep sea. In: R.W. Sims, J.H. Price and P.E.S. Whalley, *Evolution, Time and Space*. Academic Press, London, pp. 227-254.
- Hobbie, J.E., R.J. Daley and S. Jaspers, 1977. The use of nucleopore filters for counting bacteria by fluorescence microscopy. *Appl. Environmental Microbiol.*, 33: 1225-1228.
- Hollister, C.D. and B.C. Heezen, 1972. Geological effects of ocean bottom currents. In: A.L. Gordon (Editor), *Studies in Physical Oceanography*, 2: 37-66.
- Hollister, C.D., A.R.M. Nowell and P.A. Jumars, 1984. The dynamic abyss. *Sci. Am.*
- Johnson, S.B. and Y.G. Attramadal, 1982. A functional-morphological model of Tanaïs cavolinii Milne-Edwards (Crustacea, Tanaidacea) adapted to a tubiculous life-strategy. *Sarsia*, 67: 29-42.
- Jumars, P.A. and K. Fauchald, 1977. Between-community contrasts in successful polychaete feeding strategies. In: B.C. Coull (Editor), *Ecology of marine benthos*. University of South Carolina Press, Columbia, pp. 1-20.
- Jumars, P.A. and R.R. Hessler, 1976. Hadal community structure: implications from the Aleutian Trench. *J. Mar. Res.*, 34: 547-560.
- Karl, D.M., J.W. Morse and W. Sturges, 1976. Adenosine triphosphate in the North Atlantic Ocean and its relationship to the oxygen minimum. *Deep-Sea Res.*, 23: 81-88.

- Kerr, R.A., 1980. A new kind of storm beneath the sea. *Science*, 208: 484-486.
- Khripounoff, A., D. Desbruyères and P. Chardy, 1980. Les peuplement benthiques de la faille Vema: donnees quantitatives et bilan d'energie en milieu abyssal. *Oceanologica Acta*, 3: 187-198.
- Lang, K., 1968. Deep-Sea Tanaidacea. *Galathea Reports*, 9:23-209.
- Laubier, L. and M. Sibuet, 1979. Ecology of the benthic communities of the deep Northeast Atlantic. *Ambio Special Report*, 6: 37-42.
- McCave, I.N., C.D. Hollister, D. DeMaster, A. Silva, and J.Y. Yingst, in press. Internal structure and texture of a longitudinal triangular ripple. *Mar. Geol.*
- Mills, E., 1983. Problems of deep-sea biology: an historical perspective. In: G. Rowe (Editor), *Deep-Sea Biology*. Wiley, New York, N.Y. pp. 1-79.
- Munk, W., F. Snogross, and M. Wimbush, 1970. Tides off-shore: transition from California coastal to deep-sea waters. *Geophys. Fluid Dynamics*, 1: 161-235.
- Nierstrasz, H.F., 1913. Isopoda Chelifera. I. Die Isopoden der Siboga-Expedition. *Siboga-Expeditie* 32: 1-56.
- Nierstrasz, H.F. and J.H. Schuurmans Stekhoven, Jr., 1930. Ansipoda. *Die Tierwelt der Nord- Un Ostsee* 18: 134-172.
- Nowell, A.R.M., C.D. Hollister and P.A. Jumars, 1982. High Energy Benthic Boundary Layer Experiment: HEBBLE. *Eos*, 63: 594-595.
- Nowell, A.R.M., P.A. Jumars and J.E. Eckman, 1981. Effects of biological activity on the entrainment of marine sediments. *Mar. Geol.*, 42: 133-153.
- Nowell, A.R.M., P.A. Jumars and K. Fauchald, 1984. The foraging strategy of a subtidal and deep-sea deposit feeder. *Limnol. Oceanogr.*

- Rhoads, D., 1974. Organism-sediment relations on the muddy sea floor. *Oceanogr. Mar. Biol. Annual Reviews*, 12: 263-300.
- Rhoads, D.C. and L.F. Boyer, 1982. The effects of marine benthos on physical properties of sediments; a successional perspective. In: M.J.S. Tevesz and P.L. McCall (Editors), *Animal-sediment relations*. Plenum Press, New York, N.Y., pp. 31-43.
- Rhoads, D.C. and D.K. Young, 1970. The influence of deposit-feeding organisms on bottom sediment stability and community trophic structure. *J. Mar. Res.*, 28: 150-178.
- Richardson, M.J., M. Wimbush, and L. Mayer, 1981. Exceptionally strong near-bottom flows on the continental rise of Nova Scotia. *Science*, 213: 887-888.
- Romano, J.-C. and A. Dinet, 1978. Relations entre l'abondance du méiobenthos et la biomasse des sédiments superficiels estimée par la mesure des adénosines 5' phosphate (ATP, ADP, AMP). In: *Géochimie organique des sédiments marins profonds, Orgon IV, golfe d'Aden, mer d'Oman*, Ed. C.N.R.S., Paris: 159-180.
- Rowe, G.T., 1981. The deep-sea ecosystem. In: A.R. Longhurst (Editor), *Analysis of marine ecosystems*. Academic Press, New York, pp. 235-267.
- Rowe, G.T. and R.J. Menzies, 1968. Deep bottom currents off the coast of North Carolina. *Deep-Sea Res.*, 15: 711-729.
- Sanders, H.L., 1968. Marine benthic diversity: a comparative study. *Am. Nat.*, 102: 243-282.
- Sanders, H.L., R.R. Hessler and G.R. Hampson, 1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. *Deep-Sea Res.*, 12: 845-867.

- Sars, G.O., 1896. An Account of the Crustacea of Norway. II. Isopoda. Bergen Museum, Bergen. 270 pp.
- Smith, K.L., Jr., M.B. Laver and N.O. Brown, 1983. Sediment community oxygen consumption and nutrient exchange in the central and eastern North Pacific. *Limnol. Oceanogr.*, 28: 882-898.
- Thiel, H., 1983. Meiobenthos and nanobenthos of the deep-sea. In: G. Rowe (Editor), *Deep-Sea Biology*. Wiley, New York, N.Y., pp. 167-230.
- Thistle, D., 1983a. The role of biologically produced habitat heterogeneity in deep-sea diversity maintenance. *Deep-Sea Res.* 30A: 1235-1245.
- Thistle, D., 1983b. The stability-time hypothesis as a predictor of diversity in deep-sea soft-bottom communities: a test. *Deep-Sea Res.*, 30A: 267-277.
- Thistle, D. and K.M. Sherman. In preparation. The nematode fauna of a deep-sea site exposed to strong near-bottom currents.
- Watson, S.W., T.J. Novitsky, H.L. Quinby and F.W. Valois, 1977. Determination of bacterial number and biomass in the marine environment. *Appl. Environmental Microbiol.*, 33: 940-946.
- Weatherly, G.L. and E.A. Kelley, Jr., 1983. "Too cold" bottom layers at the base of the Scotian Rise. *J. Mar. Res.*, 40: 985-1012.
- Wolff, T., 1976. Utilization of seagrass in the deep sea. *Aquatic Botany*, 2: 161-174.
- Yingst, J.Y. in preparation. Relationships between organic matter availability, bacterial abundances, and benthic community structure in shelf and deep-sea environments.
- Yingst, J.Y. and R.C. Aller, 1982. Biological activity and associated sedimentary structures in HEBBLE-area deposits, western North Atlantic. *Mar. Geol.*, 48: M7-M15.

Yingst, J.Y. and D.C. Rhoads, 1980. The role of bioturbation in the environment on bacterial growth rates in marine sediments. In: K.R. Tenore and B.C. Coull (Editors), Marine Benthic Dynamics. University of South Carolina Press, Columbia, S.C., pp. 407-422.

Yingst, J.Y. and D.C. Rhoads, in press. Benthic community structure in the vicinity of the Texas Flower Gardens, Gulf of Mexico. Estuarine, Coastal, and Shelf Science.

Young, R.N. and J.B. Southard, 1978. Erosion of fine-grained marine sediments: seafloor and laboratory experiments. Bull. Geol. Soc. Am., 89: 663-672.

Figure Captions

Figure 1. Chart of the northwestern Atlantic showing the sample location (filled circle).

Figure 2. X-radiograph of vertical slab of sediment from a box core taken on the lower continental rise off Nova Scotia. Scale = 2 cm. The upper 1-2 cm of sediment is well burrowed. Differences in the degree of reworking in this zone are reflected in the density of the radiograph; the more intensely reworked areas have higher water contents (>55%) and appear lighter. Intense biogenic reworking, possibly by protobranch bivalves, is apparent as homogenized areas near the sediment-water interface on the right side of the radiograph. Small-diameter, vertically oriented tube-burrow networks are seen near the interface and larger-diameter, horizontally oriented burrows at depth. Burrows coming out of the plane of the radiograph appear as light holes. Pebbles concentrated at 1.5 cm and scattered throughout the top 10 cm illustrate the poorly sorted nature of the deposit. The pebble lag deposits reflect the presence of periodic erosional activity in this deep-sea area. (KNORR 78, Sta. 17, 4673 m, 40°21.52'N, 63°06.24'W).

Figure 3. A schematic representation of a core box showing the subsamples.

Figure 4. Median polychaete abundances versus depth for the reports in Table 1. Symbols are as follows: Hessler and Jumars (1974), filled triangles; Dahl et al. (1976), open diamonds; Jumars and Hessler (1976), filled squares; Gage (1977), filled circles; Gage (1979), open circles; Laubier and Sibuet (1979), open squares; Khripounoff et al. (1980), open triangles; this study, filled diamond. Ranges are shown for Khripounoff et al. (1980) and this study.

Figure 5. Median bivalve abundances versus depth for the reports in Table 1. Symbols as in Figure 3.

Figure 6. Median isopod abundances versus depth for the reports in Table 1. Symbols as in Figure 3.

Figure 7. Median tanaid abundances versus depth for the reports in Table 1. Symbols as in Figure 3.

Figure 8. Median nematode abundance versus depth for the reports in Table 1. Symbols are as follows: Dinet (1973), open circle; Dinet et al. (1973), open square; Coull et al. (1977), open diamond; Dinet and Vivier (1977), filled square; Dinet (1979), open triangle; George and Higgins (1979), filled circle; this study, filled diamond. Ranges are shown for Dinet and Vivier's (1977) Station 4 and for this study.

Figure 9. Median harpacticoid copepod abundance versus depth for the reports in Table 1. Symbols as in Figure 8.

Standardized correction for weight dependent interferences in ATP measurements.

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Running head: ATP recovery curves

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STANDARDIZED CORRECTION FOR WEIGHT DEPENDENT INTERFERENCES IN ATP MEASUREMENTS¹

Abstract. ATP assays can be a useful indication of microbial biomass in sediments but are subject to major analytical interferences from sedimentary constituents. A method employing standard recovery curves with heat-treated ATP-free sediment allows determination and correction for sample weight-dependent interferences in ATP extraction. This procedure is applicable to any sedimentary environment and can be used with any extraction method. Separate internal standards for each sample and multiple extractions are thereby eliminated.

Experimental microbial ecology has, in recent years, employed the measurement of cellular nucleotide concentrations and rates of nucleotide metabolism as a means of assessing biomass, growth, and activity of microbial populations (Christensen and Packard 1977; Sieburth et al., 1977; see review by Karl, 1980; Christian et al., 1982; Yingst and Aller, 1982). A number of methods for extraction of cellular nucleotides, particularly adenosine triphosphate (ATP), and innumerable improvements in these methods and in assay procedures have been developed (Borum, 1975, 1977; Schram and Stanley, 1978) with no single procedure emerging as most efficient for the spectrum of sample materials and microbial habitats that exist. Determination of the most sensitive extraction procedure and one which gives the least interference with a particular sediment type should be made. However, regardless of the extraction medium chosen, interferences unique to that chemical extractant, extraction procedure, and/or particular environmental

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substrate must be corrected for. In this paper, we describe a procedure which is applicable to any sediment extraction medium, to correct for ionic (organic and inorganic) interferences and adsorption of nucleotides onto sediment particles. This procedure sets up a one time series of standard curves for each sediment type using varying weights of ATP-free sediment from that environment. The sediment weight dependent interference is determined and used to calculate the ATP concentration of actual samples. With this approach, separate internal standard additions and extraction of each sample in triplicate in order to monitor losses resulting from the various sources of analytical interference is eliminated.

We thank R. Aller for discussions during development of this procedure and helpful comments on this manuscript, and B. Negele for technical assistance.

Sediment from each environment was first heated to kill all micro-organisms and meiofauna thereby destroying essentially all measureable ATP. Using a 'double boiler' approach, a beaker was half filled with sediment, covered with aluminum foil, and placed in a larger beaker containing water and boiling chips. The beakers were placed on a hot plate and allowed to boil for 3 to 4 hours. After cooling, the sediment was homogenized by hand mixing using a sterile spatula. Duplicate subsamples of 4 different weights within the range of 0.1 to 1.0g (wet weight), corresponding to expected weight variations from actual sediment samples, were weighed out into sterile glass scintillation vials. The dry weight equivalents were calculated after determination of the water content of the heat treated sediment. ATP standards were added next to the different weights of ATP-free sediment ranging in concentration from 10 to 100 ng ATP/ml. All samples were extracted using a boiling phosphate-citrate buffer (Bulleid, 1978) and frozen

for later analysis. Each sample extract was thawed and ATP assayed using the firefly bioluminescence procedure (see DeLuca, 1978) and an ATP photometer (SAI technology, San Diego, CA).

A standard curve was prepared for each particular sediment weight by plotting relative light emission (RLU) on the abscissa (y) versus the appropriate added ATP concentration (x) : $y = mx + b$. (1)

The slope (m) of each standard curve corresponding to one particular sediment weight (w) was then plotted against the dry weight of the sediment (w)

thereby generating a relation between standard curve slope and weight of the sample. This relation is also linear and of the form: $m = m_2w + b_2$ (2)

where m_2 is the slope of the relation; w = the dry weight of the sediment sample, and m is the slope of the standard curve from (1). This equation describes the overall relationship between light emission and source of the sediment, a relationship which is a function of various factors all of which can be related to the amount of sediment extracted. The intercept (b) for each standard recovery curve (1) is plotted against weight to examine its dependency. Since $b \approx 0$ in each case and, if no linear relationship is found between b and w, then the average intercept (\bar{b}) from all standard curves (not including the reagent curve) is calculated for use in a single standard yield relationship.

The net light emission by a sample can then be used to compute the concentration of ATP in the sample as follows:

$$\begin{aligned} \text{RLU} &= m \cdot \text{ATP} + b \\ &= (m_2 \cdot w + b_2) \cdot \text{ATP} + \bar{b} \end{aligned}$$

Solving for the ATP concentration:

$$\text{ATP} = \frac{\text{RLU} - \bar{b}}{m_2 \cdot w + b_2}$$

where w is the individual sample dry weight which must fall within the weight range covered by the standard curves (1).

For comparison, standard recovery curves for the following 5 different sedimentary environments are presented. Three of these environments represent a spectrum of nearshore estuarine sediments while the fourth and fifth represent hemipelagic deep-sea sediments. The estuarine areas include a shallow muddy iron rich ($\text{Fe}^{++} = > 5\%$) site in Mud Bay, South Carolina; an intertidal sand flat in Cooks Creek, North Inlet, South Carolina; and a subtidal station in 15 m of water in central Long Island Sound (station NWC).

The deep sea sites include a station in the HEBBLE area, Nova Scotian rise, western North Atlantic at 4820 m depth, and a station in the Panama Basin (3,990 m depth) in the Eastern Pacific. Detailed site descriptions are given elsewhere (Heath et al., 1974; Aller and Yingst, 1980; Ullman and Aller, 1980; Yingst and Aller, 1982; Aller et al., 1983; Mackin and Aller, 1984), and a summary of bulk sediment characteristics for the different areas is presented in Table 1. There is substantial variability in grain size, mineralogy, and organic matter content between sites. All these properties can affect ATP adsorption.

Standard recovery curves for the 5 environments are shown in Figures 1-6. Plots of the slope of each particular sediment weight versus the dry weight of sediment are shown in Fig. 3a for Mud Bay and as insets in other figures for the other environments. The relationship of the intercepts (b) for each recovery curve versus sediment extracted for a series of experiments with Mud Bay sediment is shown in Fig. 3b. Table 2 presents the equations for each standard recovery curve. All curves illustrate varying degrees of divergence from the reagent (no sediment) curve which can be related to the weight of sediment extracted.

The fine sand sediment from Cooks Creek (Fig. 1) showed the least amount of interference with a 14% decrease in RLU's at 50 ng/ml ATP with 0.13 g of sediment and a 34% decrease with both 0.26 and 0.39 g of sediment. Mud Bay (Fig. 2), on the other hand, showed a 37% drop in RLU's at 50 ng/ml ATP with only 0.05 g of mud, continuing to decrease by 66% with 0.18 g of mud. Long Island Sound sediment (Fig. 4) also showed marked interference, decreasing to 59% from the reagent curve value at 50 ng/ml ATP with 0.1 g of sediment and 83% at 0.5 g. The extent of interference with sediment from the HEBBLE site (Fig. 5) was initially great, dropping by 58% of the reagent value at 50 ng/ml ATP with only 0.1 g of sediment. Increasing amounts of sediment, however, only decreased the RLU's by 70%, with 0.68 g of sediment. Panama Basin sediment (Fig. 6) also showed considerable interference with a decrease of 61% in RLU's at 50 ng/ml ATP with 0.11 g of sediment, 71% with 0.23 and 83% with 0.33 g. Grain size appears to be the single most important factor influencing the extent of analytical interference with ATP measurements. The sandy Cooks Creek sediment interfered least while the silt-clay Long Island Sound and Panama Basin sediments interfered the most. High amount of Fe, substantial quantities of refractory plant debris, even relatively high organic carbon or CaCO_3 , appear to be less important than the silt-clay content.

Reducing the weight of sediment extracted would appear to be the solution for minimizing interference with most sediment types although in deep sea fine-grained sediments this may not be possible because of the relatively low ambient ATP concentrations (Yingst and Aller, 1980).

It should be emphasized that the function of the standard recovery procedure outlined in this paper is not to assess the efficiency of a given extraction medium, but rather to provide a generalized approach for

evaluating and correcting for the sum total of losses resulting from various sources of analytical interference. Furthermore, it should be noted that the optimal extraction medium to maximize ATP yield from sediment sources (Bancroft, 1976; Karl et al., 1978), may not be the most convenient (Cunningham and Wetzel, 1978; Tobin et al., 1978), have the lowest coefficient of variation (Bancroft et al., 1976; Karl and Craven, 1980), or minimize ionic interference in the final assay step (Tobin et al, 1978; Aller and Yingst, submitted).

References

- Aller, R.C., and J.Y. Yingst. 1980. Relationships between microbial distributions and the anaerobic decomposition of organic matter in surface sediments of Long Island Sound, USA. *Mar. Biol.* 56:29-42.
- Aller, R.C., J.Y. Yingst, and W.J. Ullman. 1983. Comparative biogeochemistry of water in intertidal Onuphis (polychaeta) and Upogebia (crustacea) burrows: temporal patterns and causes. *J. Mar. Res.* 41:571-604.
- Bancroft, K., E.A. Paul, and W.J. Wiebe. 1976. The extraction and measurement of adenosine triphosphate from marine sediments. *Limnol. Oceanogr.* 21:473-480.
- Borum, G.A. (ed.) 1975. ATP Methodology Seminar. SAI Technology Co., San Diego, Calif.
- _____. 1977. Second Bi-annual ATP Methodology Symposium. SAI Technology Co., San Diego, Calif.
- Bulleid, N.C. 1978. An improved method for the extraction of adenosine triphosphate from marine sediment and seawater. *Limnol. Oceanogr.* 23:174-178.
- Christian, R.R., R.B. Hanson, and S.Y. Newell. 1982. Comparison of methods for measurement of bacterial growth rates in mixed batch cultures. *Appl. Environ. Microbiol.* 43(5):1160-1165.
- Christensen, J.P. and T.T. Packard. 1977. Sediment metabolism from the northwest African upwelling system, *Deep Sea Res.* 24, 331-343.
- Cunningham, H.W., and R.G. Wetzel. 1978. Fulvic acid interferences on ATP determinations in sediments. *Limnol. Oceanogr.* 23:166-173.
- DeLuca, M.A. (ed) 1978. *Methods in enzymology*, vol. 57. Academic Press, Inc., New York.
- DeMaster, D.J. 1979. The Marine budgets of Silica and ^{32}S ; Ph.D. thesis Yale University, 308 pp.
- Folk, R.L. 1974. *Petrology of sedimentary rocks*. Hemphill Publ. Co., Austin, Texas 182 pp.
- Gaudette, H.E. and W.R. Flight, L. Toner, and D.W. Folger. 1974. An inexpensive titration method for the determination of organic carbon in recent sediments. *Jour. Sed. Petrology* 44(1) 249-253.
- Heath, G.R., T.C. Moore, and G.L. Roberts. 1974. Mineralogy of surface sediments from the Panama Basin, eastern equatorial Pacific. *J. Geol.* 82:145-160.
- Karl, D.M. 1980. Cellular nucleotide measurements and applications in microbial ecology. *Microbiol. Rev.* 44(4):739-796.

- _____, and D.B. Craven. 1980. Effects of alkaline phosphatase activity on nucleotide measurements in aquatic microbial communities. Appl. Environ. Microbiol. 40:549-561.
- Karl, D.M., and O. Holm-Hansen. 1978. Methodology and measurement of adenylate energy charge ratios in environmental samples. Mar. Biol. 48:185-197.
- Mackin, J.E. and R.C. Aller. 1984. Ammonium adsorption in marine sediments. Limnol. Oceanogr. 29(2):250-257.
- Schram, E., and P. Stanley (eds.). 1978. International Symposium on Analytical Applications of Bioluminescence and Chemiluminescence. Vrije Universiteit, Brussels.
- Schink, J.C., J.H. Stockwell, and R.A. Ellis. 1979. An improved device for gasometric determination of carbonate in sediment. Jour. Sed. Petrology 49(2) 651-653.
- Sieburth, J. McN., K.M. Johnson, C.M. Burnney, and D.M. Lavoie. 1977. Estimation of in situ rates of heterotrophy using diurnal changes in dissolved organic matter and growth rates of picoplankton in diffusion culture. Helgol. Wiss. Meeresunters. 30:565-574.
- Tobin, R.S., J.F. Ryan, and B.K. Afghan. 1978. An improved method for the determination of adenosine triphosphate in environmental samples. Water Res. 12:783-792.
- Ullman, W.J., and R.C. Aller. 1980. Dissolved iodine flux from estuarine sediments and implications for the enrichment of iodine at the sediment water interface. Geochim. Cosmochim. Acta. 44:1177-1184.
- Yingst, J.Y., and R.C. Aller. 1982. Biological activity and associated sedimentary structures in HEBBLE-area deposits, western North Atlantic Mar. Geol. 48:M7-M-15.

Table 1. Bulk sediment properties. Determined by methods of Gaudette et al. (1974) (organic carbon) Schink et al. (1979) (calcium carbonate), and by wet sieving and pipette analysis (Folk, 1974) for grain size. Values expressed as percent by dry weight of sediment.

Site	Org C	CaCO ₃	Biogenic SiO ₂	Grain size	Reference
Cook's Creek	1.0-1.1	3-4	0.8-1.3	Sandy silt	Mackin & Aller, 1984
Mud Bay	2-4	0.5-1	1.0-1.2	Silt & clay	Mackin & Aller, 1984
Long Island Sound	2-4	4-10	4-6	Silt & clay	SiO ₂ -DeMaster, 1979
Panama Basin	2-3	15-20	7-11	Clay	Mackin & Aller, 1984
HEBBLE area, Scotian Rise	0.3-0.6	13-40	1-2	Clay	SiO ₂ -DeMaster, pers. communication

Table 2. Linear regression data for each set of standard recovery curves and inset plot shown in figures 1-6 and solution for ATP calculation for each study site. $n = 8$ for each line.

Location & Figure Designation	Sediment wt. (g)(w)	Slope (m)	Intercept b	Correlation coefficient	ATP =
Cooks Creek	reagent	991.6	-4512	.99	$\frac{RLU - (-485.5)}{-900.4 \times +896.4}$
1.	0.13	827.5	-2732	.98	
	0.26	566.0	1315	.99	
	0.36	593.4	-39	.99	
Inset	-	-900.4	896.4	-.82	
Mud Bay	reagent	854.5	-2769	.99	$\frac{RLU - (-266.5)}{-583.7 \times +537}$
2. & 3.	0.05	535.0	-1740	.98	
	0.10	447.0	885	.98	
	0.20	420.6	348	.99	
	0.40	284.0	-559	.99	
Inset	-	-583.7	537	-.97	
Long Island Sound	reagent	1009.2	-1857	.99	$\frac{RLU - (385.9)}{-772 \times +489}$
4.	0.15	420.3	-1109	.99	
	0.30	176.1	897	.99	
	0.50	138.0	1369	.98	
Inset	-	-772	489	-.89	
Panama Basin	reagent	974.1	1707.5	.99	$\frac{RLU - (-505.5)}{-715.7 \times +451.5}$
5.	0.115	360.0	1281	.98	
	0.223	310.0	-1041	.99	
	0.334	203.5	-1756	.99	
Inset	-	-715.7	451.5	-.98	

Table 2. cont'd

Location & Figure Designation	Sediment wt. (g)(w)	Slope (m)	Intercept b	\bar{b}	Correlation coefficient	ATP =
Nova Scotian Rise	reagent	951.0	557		.99	$\frac{RLJ-(791.5)}{-204.5 \times +396}$
	0.11	411.0	-421		.99	
6.	0.23	362.0	331	791.5	.99	
	0.46	269.5	1134		.99	
	0.68	276.0	2122		.99	
Inset	-	-204.5	396		-.98	

Figure Legends

Fig. 1 Light emission (RLU) vs. ATP concentrations for varying weights of sediment from Cooks Creek. Inset plot shows the slope of each recovery curve vs. dry weight of sediment extracted. o = reagent, ● = sediment. Lines - linear regression through data. Equations given in Table 2.

Fig. 2 Light emission (RLU) vs. ATP concentrations for varying weights of sediment from Mud Bay. Inset plot shows the slope of each recovery curve vs. dry weight of sediment extracted. o = reagent, ● = sediment. Lines - linear regression through data. Equations given in Table 2.

Fig. 3a The slope of each recovery curve from Fig. 2 vs. dry weight of sediment. o = reagent, ● = sediment.

3b Intercepts for standard recovery curves from 3 experiments with Mud Bay sediment vs. weight of sediment extracted. o = reagent, ● = sediment.

Fig. 4 Light emission (RLU) vs. ATP concentrations for varying weights of sediment from Long Island Sound, Sta. NWC. Inset plot shows the slope of each recovery curve vs. dry weight of sediment extracted. o = reagent, ● = sediment. Lines - linear regression through data. Equations given in Table 2.

Fig. 5 Light emission (RLU) vs. ATP concentrations for varying weights of sediment from the Panama Basin. Inset plot shows the slope of each recovery curve vs. dry weight of sediment extracted. o = reagent, ● = sediment. Lines - linear regression through data. Equations given in Table 2.

Fig. 6 Light emission (RLU) vs. ATP concentrations for varying weights of sediment from the HEBBLE area, Scotian Rise. Inset plot shows the slope of each recovery curve vs. dry weight of sediment extracted. o = reagent, ● = sediment. Lines - linear regression through data. Equations given in Table 2.

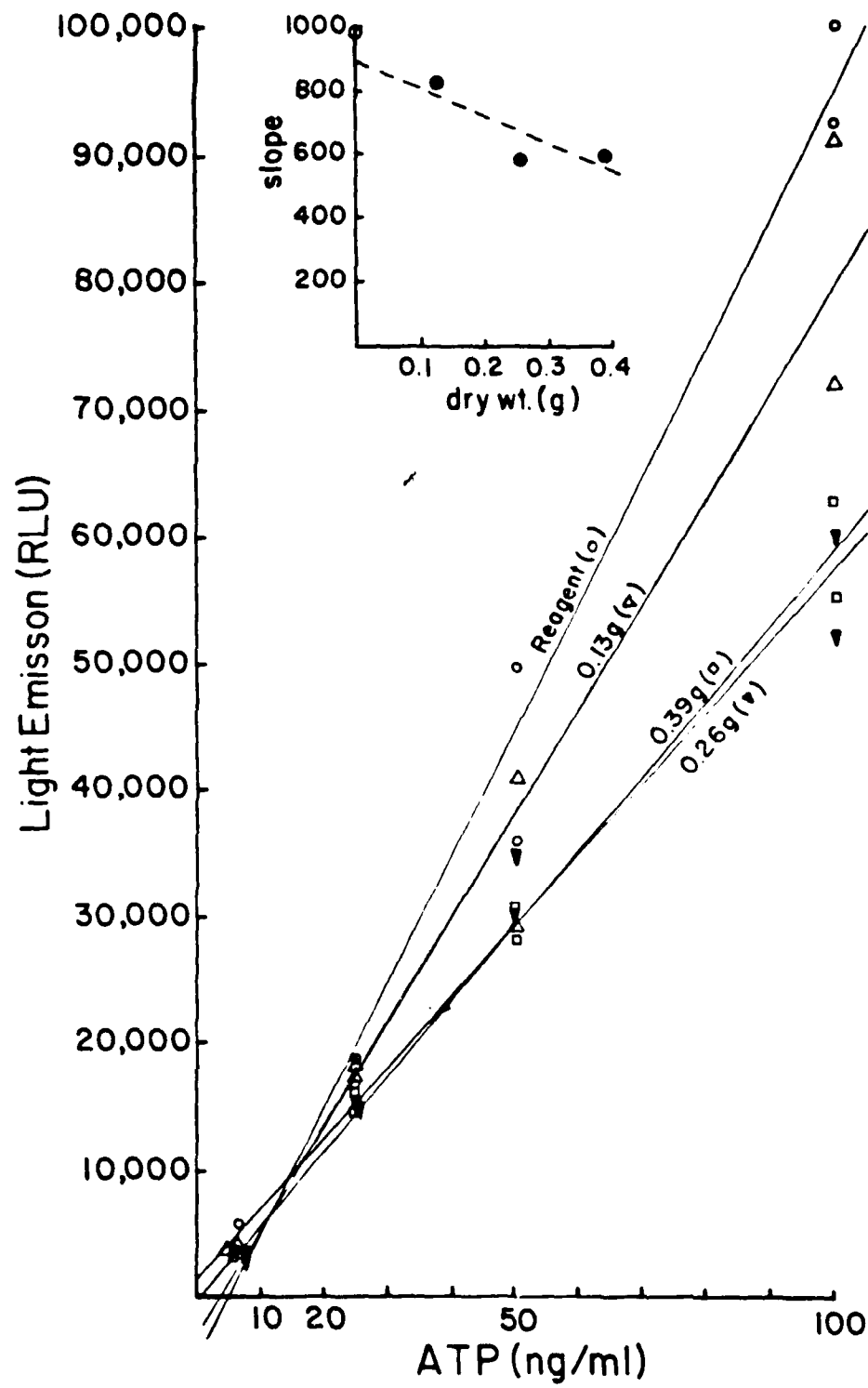


Figure 1.

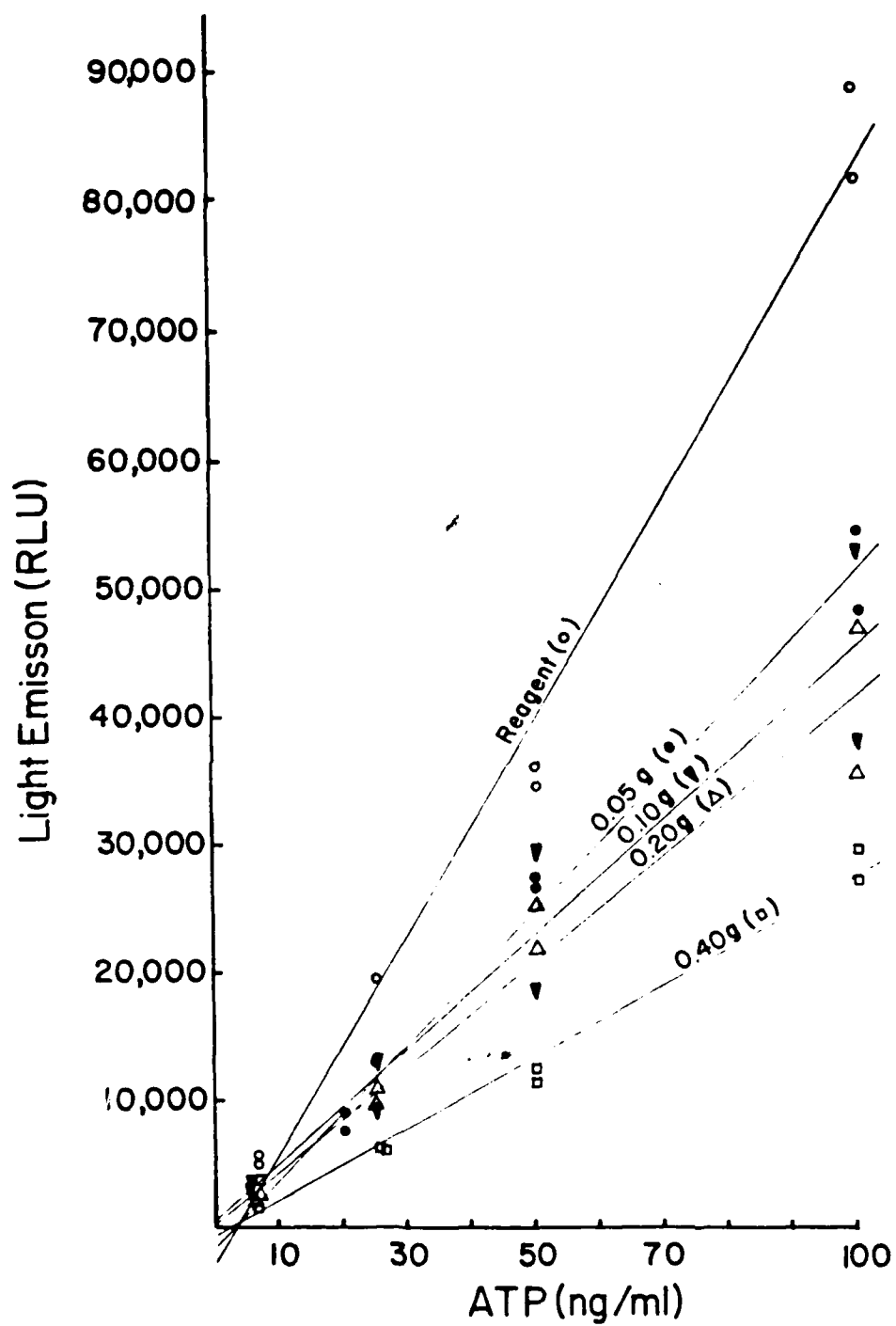


Figure 2.

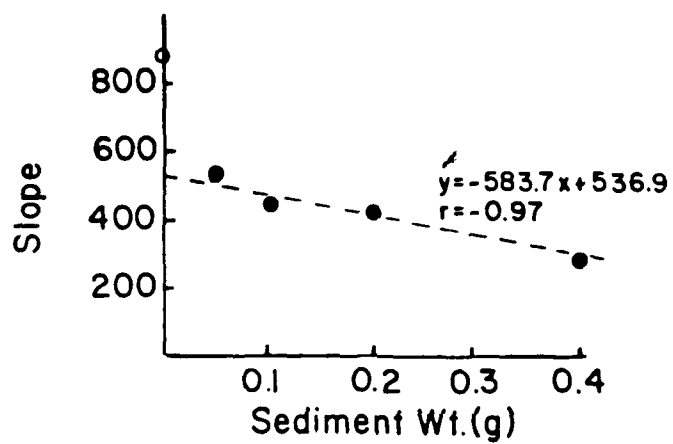
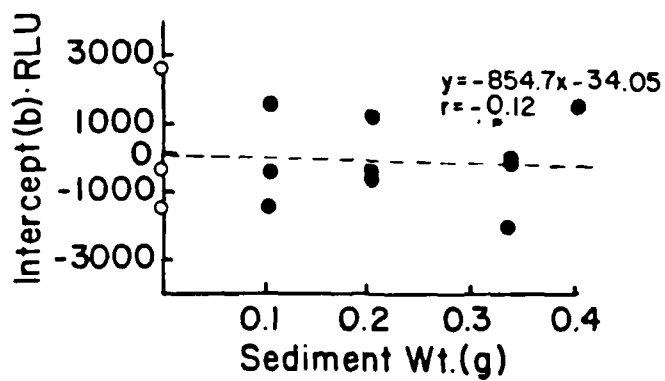


Figure 3a.



3b.

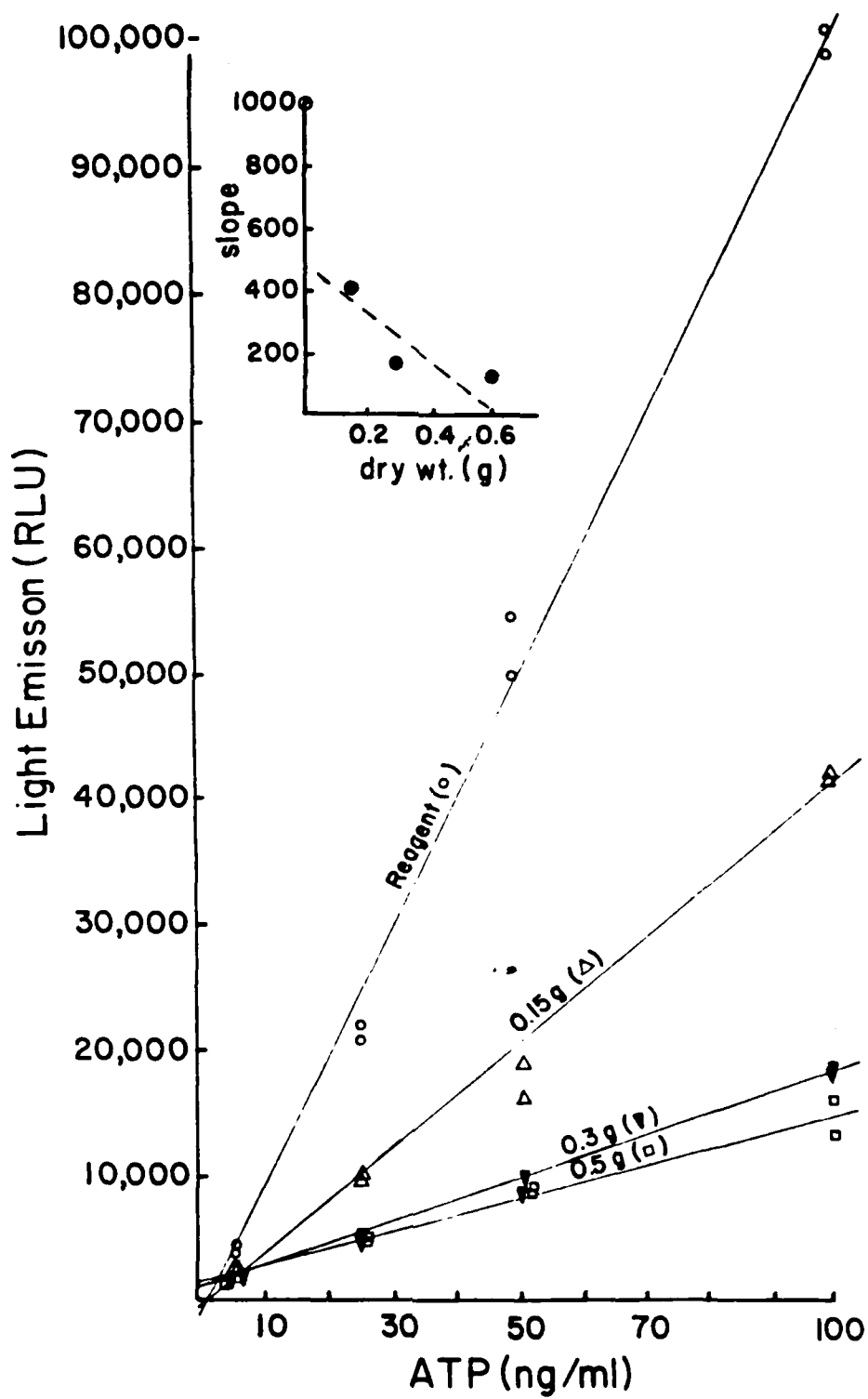


Figure 4.

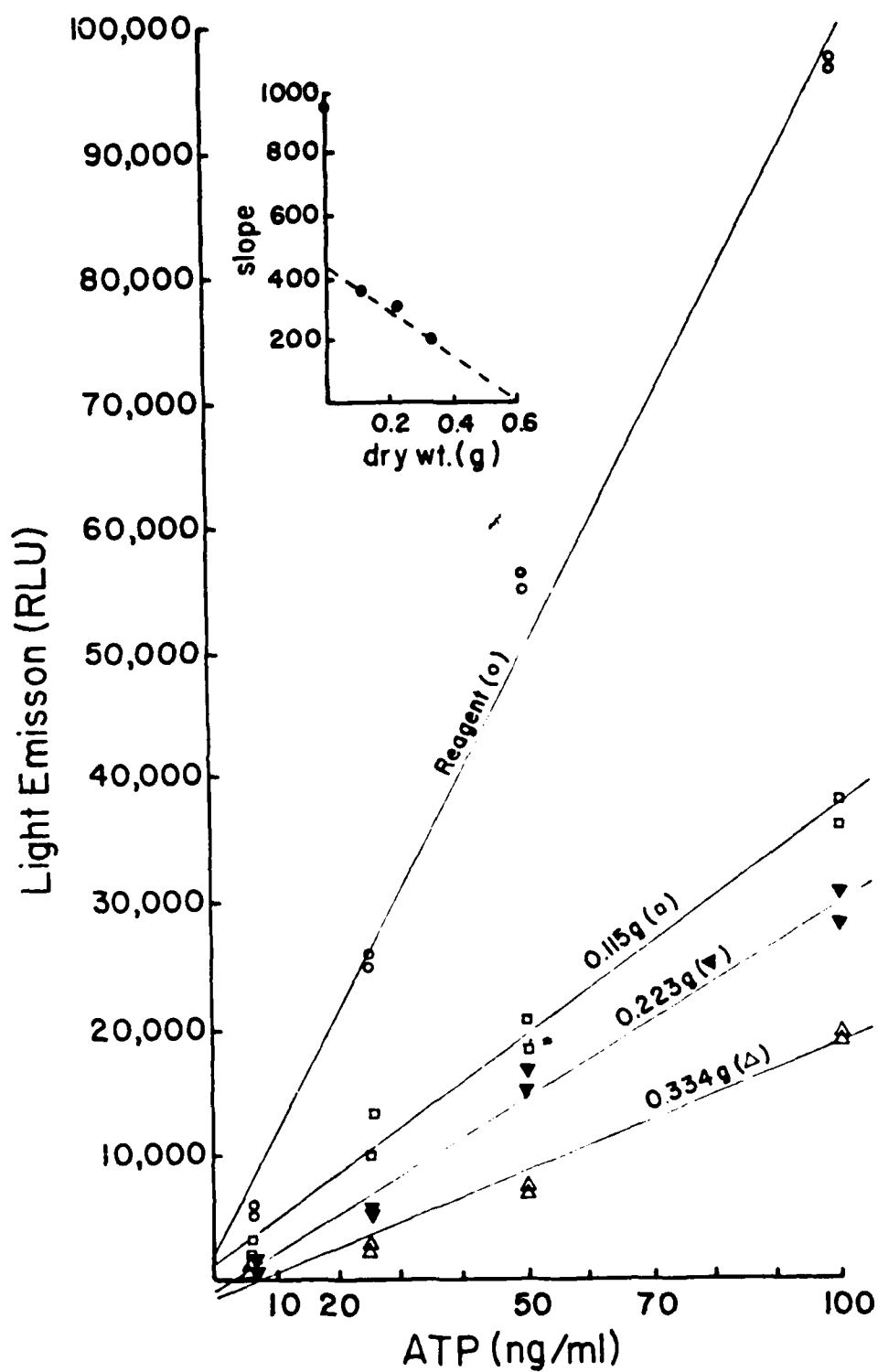


Figure 5.

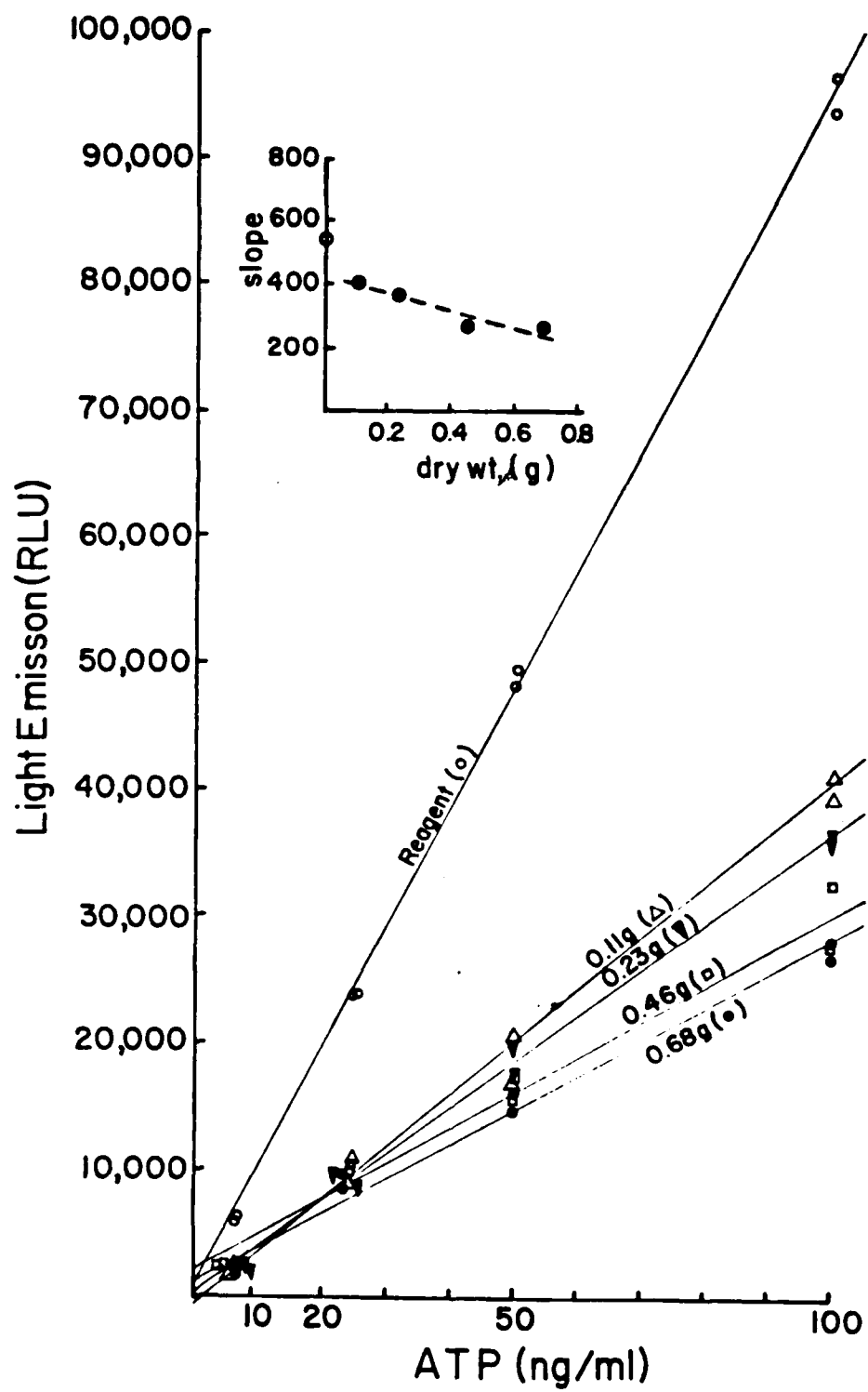


Figure 6.

**Localized Enhancement of Biological Activity Associated
with Tube and Burrow Structures in Deep-Sea Sediment:
HEBBLE Site, Western North Atlantic**

Josephine Y. Yingst¹ and Robert C. Aller²

Abstract - On the Nova Scotian Rise, relict burrows acting as traps for highly reactive relatively fresh organic matter from recent diatom blooms in surface waters are sites of intensive decomposition processes, significantly influencing sediment chemistry and the three dimensional distribution of sediment microorganisms, meio- and macroinfauna. A tube dwelling of Amphicteis sp. an apharetid polychaete and 5 burrow of various configurations obtained in box cores from depths of 4815 to 4830 m on the Nova Scotia rise were examined. In spite of the periodically strong near bottom currents which erode and physically transport sediments in this area, these burrow structures are sufficiently long lived and the response of the associated microorganisms sufficiently short that distinct biogeochemical properties occur around them.

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ANALYSIS OF A LONGITUDINAL RIPPLE FROM THE NOVA SCOTIAN CONTINENTAL RISE

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ABSTRACT

McCave, I.N., Hollister, C.D., DeMaster, D.J., Nittrouer, C.A., Silva, A.J. and Yingst, J.Y., 1984. Analysis of a longitudinal ripple from the Nova Scotian continental rise. *Mar. Geol.*, 58: 275–286.

A longitudinal ripple was obtained in a box core taken from the Nova Scotian continental rise in July 1982. Soft brown mud comprising 1.5–10% sand, ~60% silt and ~30% of <2 μm clay forms the 5 cm high and ~40 cm wide ripple. A maximum thickness of ~1 cm of this mud under the crest, thinning to 2 cm on the ripple's flank, overlies stiff muddy foram ooze. The vane shear strength of the brown mud is ~0.4 kPa whereas that of the ooze is ~4 kPa. X-radiographs show the mud to contain many fine burrows and a few larger ones as well as winnowed horizons rich in foraminifera of both benthonic and planktonic origin. Gentle wet sieving of the sand fraction on board ship showed the sand fraction to contain very few faecal pellets. Thus it appears unlikely that bedload movement played a large part in formation of the ripple. Rapid initial deposition from a concentrated suspension is suggested to have formed the structure, but this was followed by periods of erosion to yield winnowed horizons and further rebuilding with material deposited from suspension. Radiochemical data (²³²Th and ²¹⁰Pb) and X-radiographs suggest intense particle mixing ($D_B \sim 90 \text{ cm}^2 \text{ yr}^{-1}$) and rapid sediment deposition (~1.5 cm month⁻¹). Thus it is possible that the bedform (and associated structures) are destroyed and recreated on a time-scale of a few months.

INTRODUCTION

A longitudinal ripple was recovered intact and relatively undisturbed in box core BC 10 of R/V "Knorr" cruise 96 from 4820 m at 40°27.08'N 62°20.39'W on the Nova Scotian continental rise. This is the first longitudinal ripple ever obtained, though they have been photographed, observed on side-scan sonar and cored from a submersible (Heezen and Hollister,

1964, 1971; Flood, 1981; Tucholke, 1982). They are up to 0.10 m high, 0.50 m wide and 2–10 m long, are approximately symmetrical in cross-section and are aligned parallel with the dominant currents (thus “longitudinal”). On the Nova Scotian rise they occur in the area of maximum current strength and turbidity on the lower rise (Tucholke and Hollister, in prep.; Figs. 1 and 2A). Longitudinal ripples were first described by Van Straaten (1951) from tidal flats and Heezen and Hollister (1964, 1971) from the deep sea. Subsequently Flood (1981) introduced “triangular” into the name, but as nearly all ripples are triangular in cross-section we propose to revert to the original nomenclature.

The lower continental rise off Nova Scotia is the site of the High Energy Benthic Boundary Layer Experiment (HEBBLE) in which the dynamics of sediment erosion, transport and deposition are being investigated in a particularly active environment (Nowell et al., 1982). Preliminary current data show great variability with locally very high velocities along isobaths (up to 0.73 m s^{-1}) (Richardson et al., 1981) related to northerly excursions of the Gulf Stream or rings shed from it (Kelley et al., 1982). The region also shows variable but locally high turbidity (up to 12 g m^{-3}) (Biscaye et al., 1980; Spinrad and Zaneveld, 1982; McCave, 1983). The box core described here was taken as part of a systematic investigation of the $2 \times 4 \text{ km}$ HEBBLE site which included box coring and stereophotography. In this area the

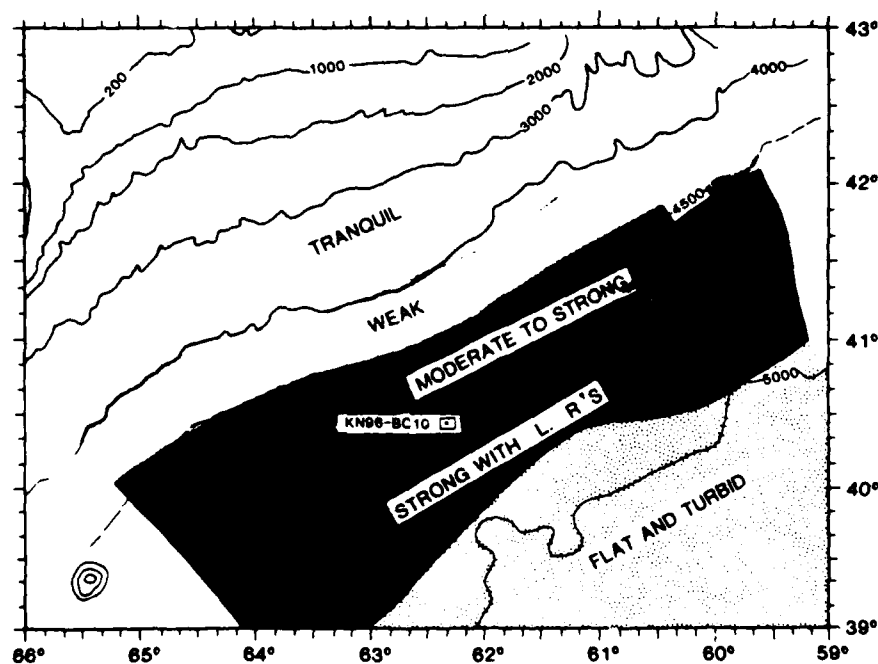


Fig. 1. Zonation of the Nova Scotian Continental Rise in terms of current strength inferred from photographed bedforms by Tucholke and Hollister (in prep.).

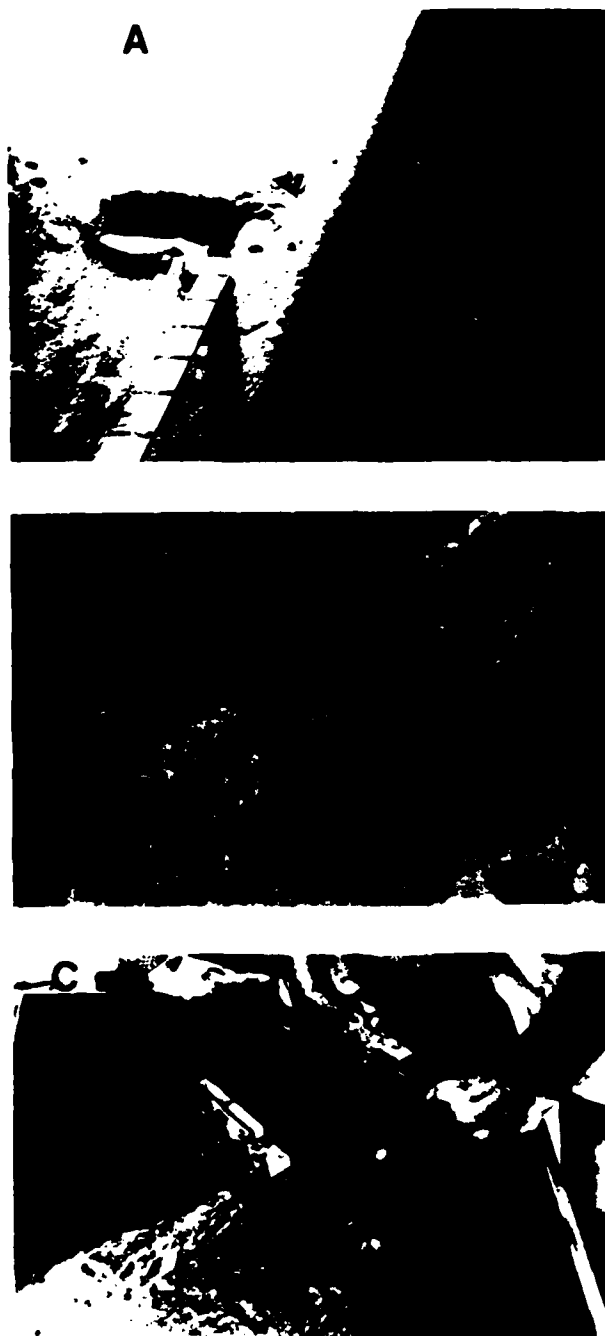


Fig.2. A. A longitudinal ripple photographed south of the HEBBLE site on the Nova Scotian rise (picture width 0.45 m). B. The ripple recovered in BC10 on 12 July 1982 (picture width 0.55 m). C. Slab corers being inserted.

uppermost 0.5–8 cm of sediment is a soft brown mud underlain by about 30 cm of muddy foram ooze which is extensively burrowed. Within the foram ooze is a silty turbidite at 20 cm depth, and at the base of the core (40 cm) another containing very coarse sand and fine gravel.

The two existing hypotheses for the origin of longitudinal ripples are: (a) that they develop rapidly (by an unspecified depositional process) under a short-lived high-velocity flow in which secondary circulation is well developed (Flood, 1981); and (b) that they are formed by deposition in the lee of biogenic mounds and extended by oblique currents which modify them in the manner of transverse bed-load ripples (Tucholke, 1982). In this paper we provide basic data on a longitudinal ripple and speculate on its origin.

DATA

Procedures

The overlying water was siphoned from the 0.5 m² box core revealing the longitudinal ripple (Fig.2B). After photographing the feature, several 25 mm thick rectangular acrylic subcorers were inserted (Fig.2C). Several cylindrical cores were also inserted. The mud was tending to liquify and flow at the surface so the tops of the flat X-ray subcores were carefully filled with salt water to provide buoyancy and inhibit this process. An area on the crest and another on the flank of the ripple were scraped to provide samples for surface grain-size analysis. Gentle wet sieving through nested nylon mesh screens was done on board. A transect across the ripple was made with a motorised shear vane capable of penetrating to about 8 cm. An excavation was then made and the shear strength profiles were extended down to a maximum depth of about 12 cm. Finally the side was removed from the box and the sub-cores were capped and extracted. The rectangular subcores were X-rayed on board ship. The resulting X-radiographs were used during subsampling for radiochemical and grain-size analyses to ensure that samples were taken parallel to sediment layers.

Form and internal structure

Cross sections show the ripple to be 4–5 cm high with a measured half-width of 20 cm and a nearly symmetrical shape (Figs.2–5). The X-radiographs (Fig.3) reveal an upper layer of soft brown mud criss-crossed with filamentous burrows <1 mm diameter, a very large burrow filled with forams under the crest and several darker (more dense) horizontal layers comprising concentrations of forams in the crest region (Fig.4). The base of the longitudinal ripple has a sharp contact with the underlying bioturbated ooze containing a few pieces of fine gravel. The interpretation of the dark (more dense) layers as foram concentrations is corroborated by observation and by size analysis (Fig.4) showing 4–5% >63 μ m in the top 3 slices but only 1.4% in slice no. 4 which contains no dark layers.

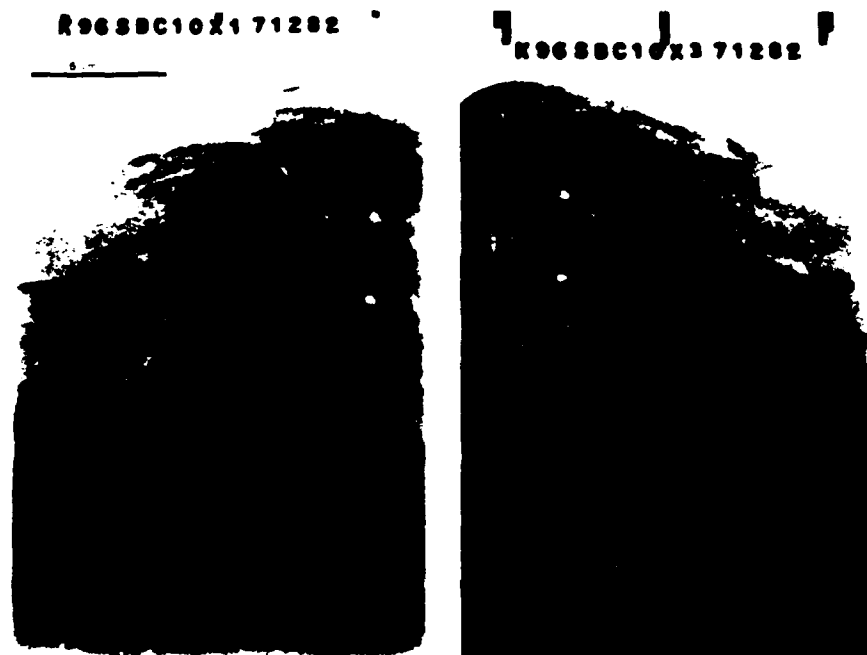


Fig.3. X-radiographs of the ripple. Darker tones mean more opaque to X-rays and probably signify zones of coarser material with lower water content.

The internal structure rules out the possibility that these features are formed by draping some underlying topographic structure. (The position of the foram-filled burrow under the crest in Figs.3 and 4 is fortuitous and was not found in all X-rayed slabs.) The darker, (denser) layer along some of the top of the lower foram ooze unit suggests that it too may have been winnowed at some time.

Grain size

The data in Table I show very little material in the sediment that is of bed load (i.e. sand) size. The uppermost scraped sample on the crest, nominally 1 mm thick, containing 26.1% sand of which >90% is foraminifera, confirms the interpretation of the dark layers on the X-radiographs (Figs.3 and 4). The lowest sample from the grain-size subcore (6–7.5 cm) includes the foram-filled burrow, resulting in an analysis showing 32.8% sand. However, most of the brown mud samples in the ripple contain $\leq 5\%$ sand. The mud fraction in the area has $\sim 35\%$ $< 2 \mu\text{m}$ clay and has a well-developed peak in the region 8–16 μm (shown by both pipette and Coulter Counter® analyses), comprising quartz with subordinate feldspar and calcite. The sand

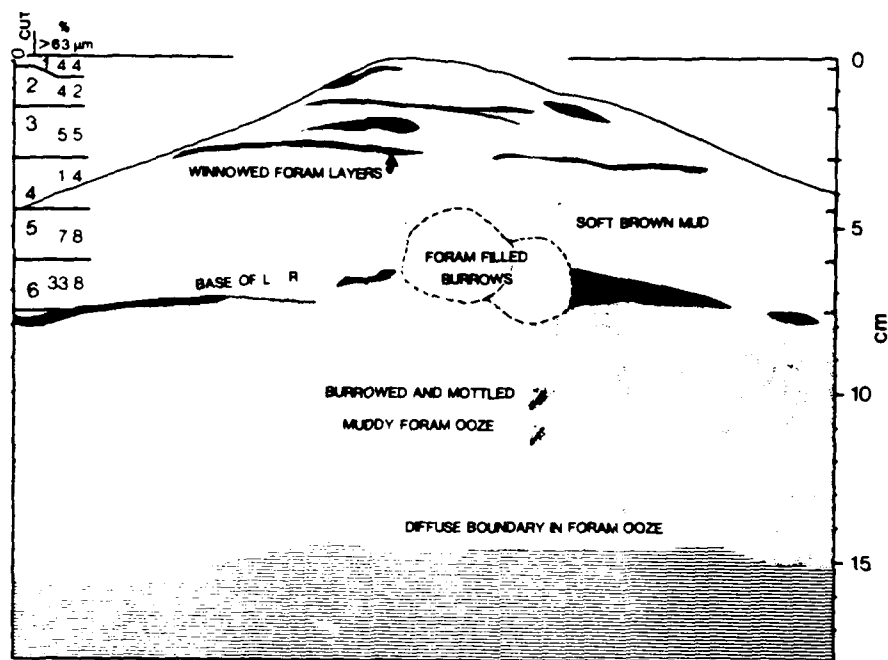


Fig.4. Internal structure of the ripple interpreted from X-radiographs and visual examination of samples and slices. The percent sand is shown on the left for six slices; note that it is higher in the region where winnowed foram layers are inferred.

fraction is almost entirely whole and broken foraminifera. There were a few faecal pellets in the freshly sieved material but these were outnumbered by small hollow brown tubes of benthic agglutinated foraminifera.

Physical properties

The vane shear strength is very uniform at 0.4 kPa through the soft brown mud but rises sharply to about 4 kPa in the muddy foram ooze. Although strength increases downwards slightly in the brown mud on some profiles (Fig.5), the unit is rather uniform and its low strength indicates that it is most unlikely to be an erosional remnant feature. Salt-corrected water content averaged over the upper 4.8 cm of the ripple is 101.4% dry weight; with particle density of 2500 kg m^{-3} this is equivalent to sediment dry bulk density of 729 kg m^{-3} .

Distribution of ^{234}Th and ^{210}Pb

Measurements of ^{234}Th ($t_{1/2} = 24$ days) and ^{210}Pb ($t_{1/2} = 22$ years) form part of a larger data set from this area which will be reported (including analytical methods) by DeMaster et al. (in prep.). The ^{234}Th data showing

TABLE I

Grain-size data

Position	Depth (cm)	% > 250 μ m	% 250-63 μ m	% 63-30 μ m	% < 30 μ m
<i>Surface, wet sieved at sea</i>					
Crest	0-0.1	24.34	1.79	1.79	72.07
	0.1-0.5	0.91	1.44	3.73	93.95
	0.5-2	1.90	2.10	2.51	93.45
Flank	0-0.1	3.75	3.25	2.20	90.80
	0.1-0.5	2.27	1.66	0.90	95.14
	0.5-2	1.35	0.39	0.20	98.07
<i>Slices, wet sieved in laboratory</i>					
X3*-1	0-0.3	1.72	2.65	4.28	91.35
X3*-2	0.3-1.5	2.52	1.72	2.76	93.01
X3*-3	1.5-3	4.35	1.14	1.86	92.66
X3*-4	3-4.5	0.72	0.69	0.98	97.62
X3*-5	4.5-6	6.02	1.77	1.29	90.93
X3*-6	6-7.5	25.93	7.88	10.0	59.28
PC-1	0-0.25	3.85	2.12	1.91	92.11
PC-2	0.25-0.5	5.75	3.27	3.24	87.74
PC-3	0.5-1	6.26	1.59	1.75	94.10
PC-4	1-2	6.53	4.12	4.24	85.11
PC-5	2-3	9.83	6.26	6.88	75.55

*See Figs.3 (right) and 4. PC was a cylindrical core inserted at the crest.

penetration to a depth of at least 5 cm have been normalized to ^{232}Th activities in order to remove the effects of variable grain size (Fig.6). The radionuclide signal may enter the seabed advectively by accumulation of sediment or diffusively by mixing (usually through biological activity). Techniques for evaluating the relative importance of mixing and accumulation in deep-sea sediments are given in DeMaster and Cochran (1982). If the ^{234}Th signal is controlled by sediment accumulation, the profile yields an accumulation rate of $S = 40 \text{ cm yr}^{-1}$. If diffusive processes control the ^{234}Th profile, the mixing coefficient (D_B) is $150 \text{ cm}^2 \text{ yr}^{-1}$.

Guinasso and Schink (1975) introduce a parameter, $G = D_B/SL$ (where L is the depth of the mixed layer) of use in evaluating the relative importance of mixing and accumulation. Based on assessments of G and X-radiographs from other environments (Nittrouer and Sternberg, 1981), a G value of ~ 1 appears appropriate for the X-radiographs shown here (Fig.3). The ^{234}Th data with $G = 1$ and $L = 5 \text{ cm}$ yield $D_B/S = 5$. The upper limiting cases are $S = 40 \text{ cm yr}^{-1}$ and $D_B = 150 \text{ cm}^2 \text{ yr}^{-1}$. Table II gives the values of S and D_B consistent with both $D_B/S = 5G$ and the advection-diffusion equation applied to the thorium distribution of Fig.6. For our preferred value of $G = 1$, $S = 1.4 \text{ cm month}^{-1}$. Even if one takes $G = 10$ (but the X-radiographs of Fig.3 show too much stratification for this to be a reasonable

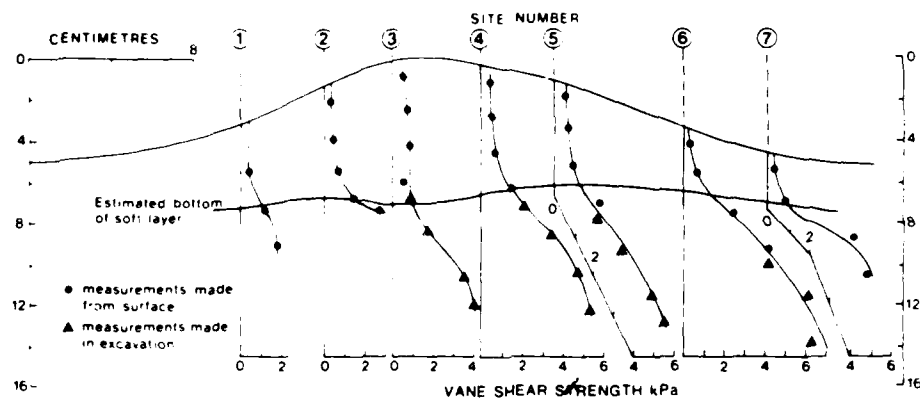


Fig. 5. Vane shear-strength profiles at seven sites across the ripple extended down into the foram ooze in an excavation where the upper mud had been removed.

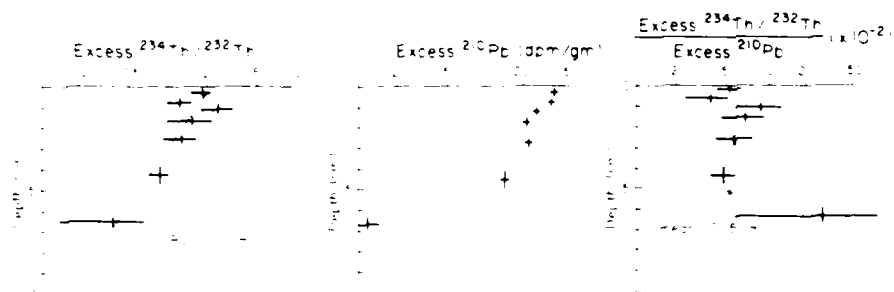


Fig. 6. Radiochemical data from an X-rayed subcore across the centre of the ripple. The lowermost sample of ^{234}Th is effectively zero. The crosses show the sampled depth range and the 1 σ error bars.

TABLE II

Values of S and D_B for varying G with $L = 5$

G	S (cm yr ⁻¹)	D_B (cm ² yr ⁻¹)
0	40	0
0.1	35.1	17.4
0.2	31.4	31.4
0.5	24	60
1	17	85
2	10.9	109
5	5.2	130
10	2.5	140
∞	0	150

value) the sedimentation rate is still $0.23 \text{ cm month}^{-1}$. Our best estimates for S and D_B in the upper soft brown mud layer are $1\text{--}2 \text{ cm month}^{-1}$ and $60\text{--}120 \text{ cm}^2 \text{ yr}^{-1}$, respectively. The mixing coefficient for the upper 5 cm is considerably higher than other values from the deep-sea ($0.04\text{--}0.2 \text{ cm}^2 \text{ yr}^{-1}$; Turekian et al., 1978; DeMaster and Cochran, 1982) or estuarine environments ($1\text{--}10 \text{ cm}^2 \text{ yr}^{-1}$; Aller and Cochran, 1976). Both biological and physical processes appear to be most important in reworking the surface sediments in the HEBBLE area (Yingst and Aller, 1982).

Under the sedimentary conditions in the upper 5 cm of the sediment column ($D_B \sim 90 \text{ cm}^2 \text{ yr}^{-1}$ and $S \sim 1.5 \text{ cm month}^{-1}$) a steady-state ^{210}Pb profile would be vertical. Figure 6 shows exponentially decreasing ^{210}Pb activity which probably results because the ^{210}Pb profile has developed in a period of a few months, rather than the 100 years necessary to achieve steady state. The fact that ^{210}Pb activity decreases with depth in the upper 5 cm requires that particle mixing must occur between high-activity surface material (sediment recently deposited from suspension) and low-activity deeper material (probably the muddy foram ooze underlying the brown mud). The near-constant $^{234}\text{Th}/^{210}\text{Pb}$ in the upper 5 cm of the longitudinal ripple indicates that the diffusive and advective processes which formed it were active on a timescale of a couple of months or less. The formation process, however, could have occurred a few months prior to core collection (with no subsequent reworking or accumulation) and still have produced a constant profile of $^{234}\text{Th}/^{210}\text{Pb}$.

INTERPRETATION

The ripple is vertically uniform in physical properties, contains thin foraminiferal horizons probably produced by winnowing, but otherwise little material that was bedload. Radiochemical data show that the sediment was deposited in a period of a few months prior to core collection. These data also indicate that particle reworking, probably by infauna, has mixed some old material from below into the recently deposited mud. The overall rate of deposition is less than 3 cm month^{-1} , probably between 1 and 2 cm month^{-1} , coupled with an extremely high mixing coefficient of $60\text{--}120 \text{ cm}^2 \text{ yr}^{-1}$.

Two possible interpretations of these basic data are first, the bedform accreted continuously over 3 months at $\sim 1.5 \text{ cm month}^{-1}$. This would be a maximum of 4.5 cm in 90 days or 0.05 cm day^{-1} equivalent to $0.36 \text{ kg m}^{-2} \text{ day}^{-1}$ for sediment with deposited density 729 kg m^{-3} . However, if one takes the mean deposit thickness across the 0.40 m width of the feature to be 1.5 cm , then a mean accumulation rate is $0.12 \text{ kg m}^{-2} \text{ day}^{-1}$, the figure that will be used here. The second possibility is that accretion occurred in several episodes of very rapid deposition, each followed by a period of erosion (producing the foram layers) and biological reworking.

Sediment fluxes for the HEBBLE area can be estimated using engineering data from estuarine muds and the deposition equation $R = [C_b u_* (1 - \tau_o/\tau_{*1})]$.

where R is the instantaneous rate of deposition, C_b the near-bed concentration, w_s the particle settling velocity, τ_o the bed shear stress and τ_l the limiting stress for deposition. Several authors have demonstrated that sediment settling velocity is a function of concentration (e.g. Owen, 1971), and thus a twofold increase in concentration may result in at least a fourfold increase in deposition rate. Taking values from the middle of the range of estuarine data $w_s = 0.5C \text{ mm s}^{-1}$, and with $C = 0.05 \text{ kg m}^{-3}$ then $w_s = 0.025 \text{ mm s}^{-1}$ (McCave, 1984). Assuming a low shear stress during deposition, say $\tau_o = 0.016 \text{ Pa}$ (shear velocity $u_* = (\tau_o/\rho)^{1/2} = 0.4 \text{ cm s}^{-1}$ corresponding to a current of $\sim 11 \text{ cm s}^{-1}$), and a limiting depositional stress $\tau_l = 0.08 \text{ Pa}$ then the rate of deposition is $10^{-6} \text{ kg m}^{-2} \text{ s}^{-1}$ or $0.086 \text{ kg m}^{-2} \text{ day}^{-1}$. Thus in order to fulfill the first possible interpretation, deposition would have to be continuous from a nepheloid layer of concentration $50\text{--}60 \text{ g m}^{-3}$ for 90 days. To date the highest measured concentration from the HEBBLE area has been 12 g m^{-3} (Biscaye et al., 1980) and a $4\text{--}16 \text{ g m}^{-3}$ maximum was recorded nearby at a depth of 5200 m by Amos and Gerard (1979). Optical records show the concentration to be extremely variable in the HEBBLE area (Pak and Zaneveld, 1983), thus periods of constant 50 g m^{-3} for three months are extremely improbable. An origin by continuous deposition over 90 days is most unlikely. For the alternative of fast episodic deposition, increased concentration results in greater settling velocity — a concentration of 400 g m^{-3} yields a settling velocity of 0.20 mm s^{-1} . Under the same stress conditions as above, this gives $R = 5.5 \text{ kg m}^{-2} \text{ day}^{-1}$. At that rate the required 10 kg m^{-2} can be deposited in less than two days.

Such high concentrations have never been measured, but a 1 m path-length transmissionmeter in the HEBBLE area has registered periods of less than 0.01 percent transmission, equivalent to concentrations in excess of 10 g m^{-3} (Pak and Zaneveld, 1983). Concentrations an order of magnitude greater under high velocities, yielding conditions usually associated with estuaries, are not inconceivable.

In order to deposit that much material it must first be eroded. An erosion rate constant M appropriate to mud of 150 percent water content is $\sim 0.3 \times 10^{-3} \text{ s m}^{-1}$ in the equation giving erosion rate $\dot{e} = M(\tau_o - \tau_c) \text{ kg m}^{-2} \text{ s}^{-1}$ in which τ_c is the critical erosion stress. In a high stress event with $\tau_o \sim 0.65 \text{ Pa}$ ($u_* = 2.5 \text{ cm s}^{-1}$) and $\tau_c \sim 0.5 \text{ Pa}$, $\dot{e} = 3.9 \text{ kg m}^{-2} \text{ day}^{-1}$ or 0.65 cm day^{-1} . Thus a centimeter could be eroded within two days to yield a high-concentration suspension. Following a drop in current speed this would rapidly deposit sediment. The event involving both erosion and deposition need not take longer than one to two weeks. A current meter at 59 m above the bed 2 km from the box core at the HEBBLE site recorded several episodes of rapid flow up to a day-averaged value of 0.27 m s^{-1} in velocity and including at least four periods of flow $< 0.05 \text{ m s}^{-1}$ between April and July 1982 (Koenig et al., 1983). The highest speeds here are not likely to have produced the required erosion, but this could well have occurred several kilometers or tens of kilometers upstream.

Because all evidence suggests variable suspended sediment concentrations the preferred scenario is one of intense erosion events followed by a drop in current speed and rapid deposition with development of longitudinal ripples. These form quickly and are presumed to achieve their fairly regular spacing because of a helical flow structure in some boundary layer (Flood, 1981). To account for a 5–10 m spacing with symmetrical helices such a layer would need to be 2–5 m thick and might correspond to the log-layer height or could be a sediment-stratified layer. This explanation has features in common with that of Flood (1981) but does not support Tucholke's (1982) proposal that the features grow as quasi-transverse bedload ripples, though they may well nucleate in the lee of biological mounds. The features, once formed, are subject to subsequent minor episodes of erosion which remove their tops and then, in the succeeding deposition phase, are built up again. At this time however they may well resemble transverse ripples, particularly during the phase when a winnowed foram cap develops.

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REFERENCES

- Aller, R.C. and Cochran, J.K., 1976. $^{234}\text{Th}/^{238}\text{U}$ disequilibrium in near-shore sediment: particle reworking and diagenetic timescales. *Earth Planet. Sci. Lett.*, 29: 37–50.
- Amos, A.F. and Gerard, R.D., 1979. Anomalous bottom water south of the Grand Banks suggests turbidity current activity. *Science*, 203: 894–897.
- Biscaye, P.E., Gardner, W.D., Zaneveld, J.R.V., Pak, H. and Tucholke, B.E., 1980. Nephels! have we got nephels! *EOS, Trans. Am. Geophys. Union*, 61, 1014 (abstract).
- DeMaster, D.J. and Cochran, J.K., 1982. Particle mixing rate in deep-sea sediments determined from excess ^{210}Pb and ^{210}Po profiles. *Earth Planet. Sci. Lett.*, 61: 257–271.
- Flood, R.D., 1981. Longitudinal triangular ripples in the Blake–Bahama Basin. *Mar. Geol.*, 39: M13–M20.
- Guinasso, N.L. and Schink, D.R., 1975. Quantitative estimates of biological mixing rates in abyssal sediments. *J. Geophys. Res.*, 80: 3032–3043.
- Heezen, B.C. and Hollister, C.D., 1964. Deep-sea current evidence from abyssal sediments. *Mar. Geol.*, 1: 141–174.
- Heezen, B.C. and Hollister, C.D., 1971. *The Face of the Deep*. Oxford University Press, New York, N.Y., 659 pp.
- Kelley, E.A., Weatherly, G.L. and Evans, J.C., 1982. Correlation between surface Gulf Stream and bottom flow near 5000 meters depth. *J. Phys. Oceanogr.*, 12: 1150–1153.
- Koenig, P., Harkema, R. and Weatherly, G.L., 1983. A compilation of moored current meter data in HEBBLE area, October 1980–October 1981. Florida State Univ., Tallahassee, Fla., Dept. of Oceanography, Tech. Rept. 83-01, 92 pp.

- McCave, I.N., 1983. Particulate size spectra, behaviour and origin of nepheloid layers over the Nova Scotian Continental Rise. *J. Geophys. Res.*, 88: 7647-7666.
- McCave, I.N., 1984. Erosion, transport and deposition of fine-grained marine sediments. In: D.A.V. Stow and D.J.W. Piper (Editors), *Deep Sea Fine-Grained Sediment Transport*. Geol. Soc. London, Spec. Publ., pp. 35-69.
- Nittrover, C.A. and Sternberg, R.W., 1981. The formation of sedimentary strata in an allochthonous shelf environment: the Washington continental shelf. *Mar. Geol.*, 42: 201-232.
- Nowell, A.R.M., Hollister, C.D. and Jumars, P.A., 1982. High energy benthic boundary layer experiment, HEBBLE. EOS, Trans. Am. Geophys. Union, 63: 594-595.
- Owen, M.W., 1971. The effect of turbulence on the settling velocities of silt flocs. *Proc. 14th Congress Int. Assoc. Hydraulics Res.*, Paris, Paper D-4, pp. 27-32.
- Pak, H. and Zaneveld, J.R.V., 1983. Temporal variations of beam attenuation coefficient on the continental rise off Nova Scotia. *J. Geophys. Res.*, 88: 4427-4432.
- Richardson, M.J., Wimbush, M. and Mayer, L., 1981. An exceptionally strong near-bottom current on the continental rise of Nova Scotia. *Science*, 213: 887-888.
- Spinrad, R. and Zaneveld, J.R.V., 1982. An analysis of the optical features of the near-bottom and bottom nepheloid layers in the area of the Scotian Rise. *J. Geophys. Res.*, 87: 9553-9561.
- Tucholke, B.E., 1982. Origin of longitudinal triangular ripples on the Nova Scotian continental rise. *Nature*, 296: 735-737.
- Turekian, K.K., Cochran, J.K. and DeMaster, D.J., 1978. Bioturbation in deep-sea deposits: rates and consequences. *Oceanus*, 21(1): 34-41.
- Van Straaten, L.M.J.U., 1951. Longitudinal ripple marks in mud and sand. *J. Sediment. Petrol.*, 21: 47-54.
- Yingst, J.Y. and Aller, R.C., 1982. Biological activity and associated sedimentary structures in HEBBLE-area deposits, western North Atlantic. *Mar. Geol.*, 48: M7-M15.

Letter Section

**BIOLOGICAL ACTIVITY AND ASSOCIATED SEDIMENTARY
STRUCTURES IN HEBBLE-AREA DEPOSITS, WESTERN NORTH
ATLANTIC**

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ABSTRACT

Yingst, J.Y. and Aller, R.C., 1982. Biological activity and associated sedimentary structures in HEBBLE-area deposits, western North Atlantic. *Mar. Geol.*, 48: M7–M15.

Biological and sedimentologic samples along with X-radiographs of sediment slabs were taken from box cores in the HEBBLE area (4700 m) on the lower continental rise of Nova Scotia. These data suggest that this bottom region is influenced by periods of strong near-bottom currents which erode and physically transport sediments. These high periods alternate with periods of weaker flow. Biogenic reworking of sediments by an active benthic infauna dominates particle transport during low flow conditions.

INTRODUCTION

The activities of bottom-dwelling organisms modify the physical and chemical properties of sediments very near the sediment–water interface and thereby influence the erodibility of the sediment surface. Our understanding of how biological processes influence erosion and sediment transport as well as those which help structure the sediment surface are based mostly on shallow water studies (Jumars et al., 1981; Nowell et al., 1981; Rhoads and Boyer, in press) and suggest that the activities of macro-, meio-, and microorganisms are all involved. Little is known about animal–sediment relations in the deep-sea, particularly organism–sediment–flow interactions (Nowell et al., 1981). It is often assumed that because of low food supply in the deep-sea, biological activity is minimal and of comparatively little consequence in altering sediment properties. As part of the biology component of the High-Energy Benthic Boundary Layer Experiment (HEBBLE) (Kerr, 1980), we are examining this assumption by studying the biological community and animal–sediment relations in an area affected by high-velocity near-bottom currents. Current-meter measurements across the HEBBLE study area on the lower continental rise of Nova Scotia (39–43°N, 59–66°W)



Fig. 1. Seafloor on lower continental rise of Nova Scotia in HEBBLE area at 4734 m, downslope 35 km from the location of X-radiographs from BC 6 and 31 km from BC 9 (Fig. 2). The presence of strong near-bottom currents in this area is indicated by relatively little surficial evidence of biological activity, the absence of a flocculent surface sediment layer, and the presence of small-scale crag and tail features. The photograph was taken with a stereo camera system positioned 100 cm above the sediment surface. White portion of scale bar at lower left = 5 cm. Mud clasts on sediment surface are the result of the camera legs impacting the seafloor. (KNORR 83, Oct. 1980, Sta. 2; 40° 22.2' N; 62° 44.7' W.) Photo courtesy of C. Hollister and S. Swift.

(Hollister and Heezen, 1972; Tucholke et al., 1979) have recorded current speeds in excess of 35 cm/sec at 50 m above the bottom for periods of several days with a maximum recorded speed of 73 cm/sec. These are among the highest current velocities ever measured in the deep-sea (Richardson et al., 1981). In addition, sediment-trap collections and transmissometer readings in the HEBBLE area show high concentrations of particulate matter in the water for 2 m overlying the bottom, presumably the result of erosion and suspension of surface sediments by the strong near-bottom currents (Biscaye et al., 1980).

Bottom photographs from hundreds of camera lowerings in addition to hundreds of kilometers of Deep-Tow coverage with side-scan sonar indicate that the seafloor between 4600 and 5000 m in the HEBBLE study area is comprised of migrating, longitudinal triangular ripples of various size scales with crag and tail features between and on the ripples (Tucholke et al., 1980). The term crag and tail refers to an irregularity in the sediment surface where sediment is shaped into tails behind pebbles, feces, mud clasts or other resis-

tant objects by currents (see fig. 9.7, p. 340 in Heezen and Hollister, 1971). There is relatively little obvious surficial evidence of biological activity such as feeding traces, feeding voids, fecal mounds, burrow openings, or exposed tubes in these rippled bottom areas (Fig. 1). Such surficial biogenic sedimentary structures are readily evident in deep-sea regions of apparently weaker current flow (Heezen and Hollister, 1971).

METHODS

In order to evaluate the possible influences of animal activities on sediment transport in the study area, biological samples and X-radiographs of vertical sediment slabs from box cores were taken in a rippled region during April–May 1980 (Fig. 2A, B and C). Biological and sedimentological samples, and X-radiographs of sediment slabs were obtained in water depths ranging from 4600 to 4700 m from four 0.25 m² USNEL box cores (Hessler and Jumars, 1974) (with the "Sandia" modification for decreasing the impact of the bow wave) which were internally partitioned into either 4 or 25 square subcores. Once aboard ship, each subcore was subsampled vertically to a depth of 10 cm for sedimentologic analyses. Sediment from each depth interval was homogenized in sterile petri dishes by gentle hand mixing using sterile spatulas and then apportioned for the various analyses. Water content was determined by weight losses of wet sediment dried at 60°C. Bulk density was determined from weight losses of known volumes of wet sediment dried at 60°C. Organic carbon was determined by wet oxidation using a modified Walkey-Black titration method (Gaudette et al., 1974; precision $\pm 1\%$). Total nitrogen was measured using a Coleman CHN analyzer. Yields of $96 \pm 0.035\%$ were obtained by five determinations of standards; all samples were corrected to 100% using this factor.

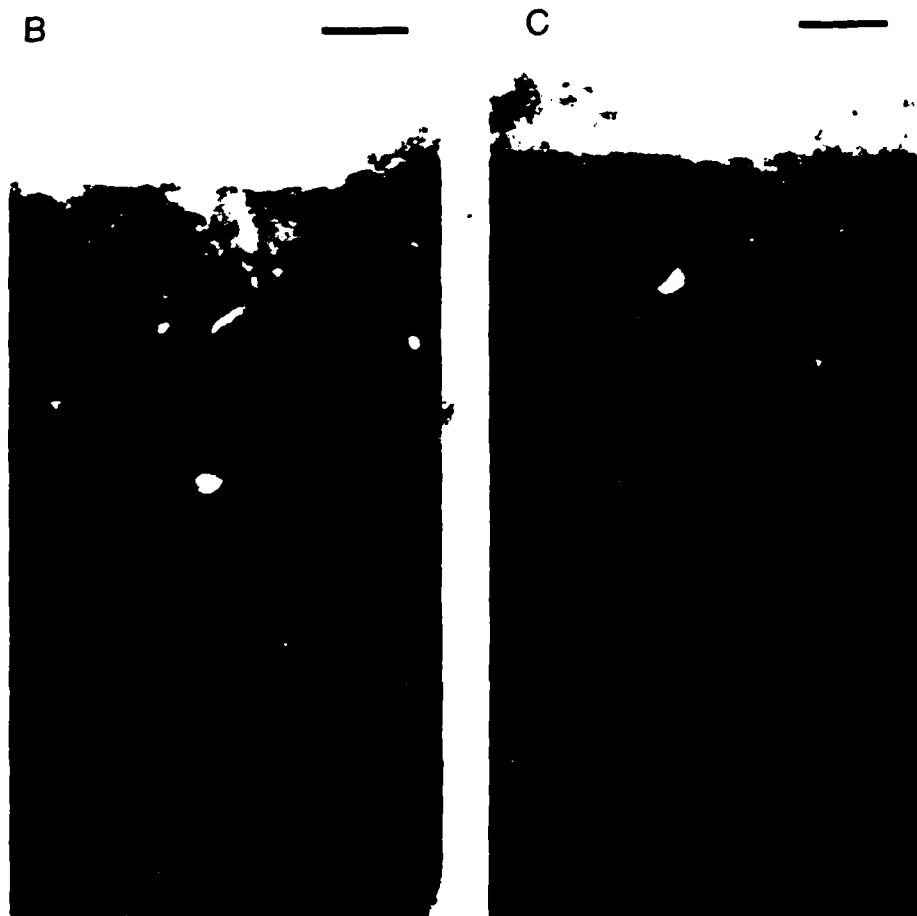
Bacteria were counted directly from glutaraldehyde preserved subsamples (0.3% glutaraldehyde in 3% NaCl) using the epifluorescence method of Hobbie et al. (1977) as modified by Watson et al. (1977) (see Aller and Yingst, 1980, for details). Sediment adenosine triphosphate (ATP) concentrations were determined aboard ship as soon after sample collection as possible, usually < 4 h, using either the boiling sodium bicarbonate method of Christian et al. (1975) or the boiling phosphate buffer method (Bulleid, 1978). All samples were extracted in triplicate. A time series of extractions showed no significant difference in samples kept refrigerated and extracted within 12 hours of collection. The efficiency of ATP recovery was determined by standard addition and all values corrected to 100% yield. There was no significant difference between samples extracted with the two buffers, and all values were used in calculating average concentrations (Yingst, in prep.). Narrow (2.5 cm) rectangular acrylic corers (Aller, 1980) were used to obtain undisturbed vertical sections of sediment from the box core. These subcores were X-rayed to provide information about macro-infaunal distributions, estimate the depth and nature of biogenic sediment reworking, and

M10

A



Fig. 2. X-radiographs of vertical slabs of sediment from box cores taken in the HEBBLE area on the lower continental rise of Nova Scotia. Scale = 2 cm. A. The upper 2–3 cm of sediment is well burrowed. Differences in the degree of reworking in this zone are reflected in the density of the radiograph, the more intensely reworked areas have higher water contents ($> 55\%$) and appear lighter. Variations in the thickness of the less dense surface zone may result from the filling-in of natural topography by a mobile sediment layer or from migrating bedforms. The abundant small-diameter burrows that criss-cross the upper few centimeters are replaced by larger and predominantly horizontally oriented burrows at depth. Burrows coming out of plane of the radiograph appear as light holes. Pebbles visible in the top few centimeters as dark objects reflect the poorly sorted nature of the deposits. (KNORR 78, Sta. 14, 4617 m, $40^{\circ} 24.37' N$, $63^{\circ} 09.52' W$.) B. This X-radiograph from the same box core as A shows two scales of layering in these deposits: fine laminations about 1–2 mm in width are visible near the sediment surface and large layers, 3–5 cm thick occur throughout the deposit. Vertical and horizontal burrow networks most dense near the sediment surface criss cross the top 5 cm. The presence of tubes and burrows near the interface in addition to the preservation of layering within this reworked zone suggest recent biogenic activity and predominantly surface deposit-feeding organisms rather than highly mobile subsurface feeders which would homogenize the sediment and tend to obliterate structures (KNORR 78, Sta. 14, 4617 m, $40^{\circ} 24.37' N$, $63^{\circ} 09.52' W$.) C. Intense biogenic reworking is apparent as homogenized areas near the sediment–water interface on the left side of the radiograph and at depth, particularly below 6 cm. Small diameter, vertically oriented tube-burrow networks are seen near the interface and larger diameter horizontally oriented burrows at depth. Note pebble-lag layer at base of comparatively watery surface zone at 2 cm near right of radiograph. This appears to be a physical feature as it is not associated with a particular biogenic structure. The presence of pebbles at 2 cm illustrates the poorly sorted nature of the deposit. Pebble-lag deposits reflect the presence of periodic erosional activity in this deep-sea area. (KNORR 78, Sta. 17, 4673 m, $40^{\circ} 21.52' N$, $63^{\circ} 06.24' W$.)



further document physically produced structures within the deposit and at the sediment surface. These X-ray cores were kept refrigerated and X-rayed on board ship within a few hours of collection.

RESULTS AND DISCUSSION

The sediment surface was sharply delimited within the box core; little flocculent material was observed on the sediment surface. Also, water overlying the sediment surface was clear in all of the subcores, indicating that resuspension did not occur during recovery of the box cores. Apparently the surface flocculent layer, if it existed, was removed as rapidly as it was produced, or prevented from forming by bottom currents. The sediments in this area are consolidated compared with shallow-water deposits of similar grain size.

TABLE I

Water content and bulk density of sediment from box core 6, KN78 Sta. 14 4617M, HEBBLE area. Bulk density determined from one 100 cm³ subcore

Depth (cm)	H ₂ O (%) X ± S.D.	No. 100 cm ³ Subcores sampled	Bulk density (g/cc dry sed.)
0-1	57.4 ± 1.9	9	0.689
1-2	51.1 ± 2.0	9	0.924
3-5	45.7 ± 1.1	4	0.837
5-7	43.7 ± 4.4	4	1.075
7-10	41.6 ± 2.9	4	0.684

Water contents range from 60% at the sediment surface to 42% at 10 cm in all box cores (Table I), and bulk densities between 0.65 and 1.00 g/cc dry sediment (Table I). Sediments are poorly sorted and are largely comprised of silt and clay-sized particles mixed with particle aggregates such as fecal pellets and larger particles such as foraminiferan tests and glacially rafted pebbles.

The X-radiographs reveal that within the upper 10-20 cm of sediment there are physically produced layers as well as extensive networks of tubes and burrows and localized deeper zones homogenized by intensive biogenic reworking (Fig. 2A, B, C). Two scales of layering are apparent. The larger sediment layers are approximately 3-5 cm thick and presumably represent changes in the type and amount of source material transported by bottom currents from upstream in addition to physical reworking by these currents. Fine horizontal laminations on the order of ~1 mm are also present in the top few centimeters of the sediment. These vary in occurrence from one part of a large box core (0.25 m²) to another and may be the result of migrating bedforms within this region. The laminations are not an artifact of sampling because they are transected by burrow networks (Fig. 2A).

Tubes and burrows criss-cross the upper 10 cm of sediment. The majority of these are probably formed by polychaete worms which numerically dominate the macrofauna (Thistle, in prep; Yingst, in prep). Macrofaunal population abundances are themselves indirect evidence of relatively high biological activity in this area. Numerical densities of comparable groups of macro- and meio-infauna appear to be 20 times higher per m² than reported from other deep-sea deposits of similar depths by Hessler and Jumars, 1974 (D. Thistle, pers. commun., 1981).

Most of the infauna appear to be surface rather than deep-feeding deposit-feeders because there is no evidence of feeding voids or feeding "pockets" at depth filled with coarser-grained particles (Rhoads, 1974). The presence of occupied and relict biogenic structures like tubes and burrows within the physically reworked regions of the box cores suggests that physical sediment erosion and transport by bottom currents is intermittent.

The vertical distribution of macrofauna, meiofauna and micro-organisms as well as the types of macrobenthos found in sieved sediment samples are consistent with the sedimentary fabric as observed from the X-radiographs. Macro- and meiofauna are most abundant in the top 2–3 cm (Thistle, in prep.; Yingst, in prep.). Sediment layers > 3 cm in thickness, which are formed by intermittent large-scale physical events are therefore preserved as this thickness exceeds the bioturbation depth. Many of the polychaetes are also tube builders and, as mentioned previously, are probably surface deposit and suspension feeders; these are life modes indicative of food sources supplied laterally by relatively strong bottom currents.

Although the presence of strong near-bottom currents causes erosion of particles and particle aggregates from the sediment surface, these currents may supply more suspended organic material to HEBBLE area deposits than is normally supplied to other deep-sea localities at comparable depths. Metabolizable organic matter passing over the sediment surface is presumably captured and mixed downward into the sediment by the burrowing and tube dwelling infauna. Evidence for a relatively elevated supply comes from the

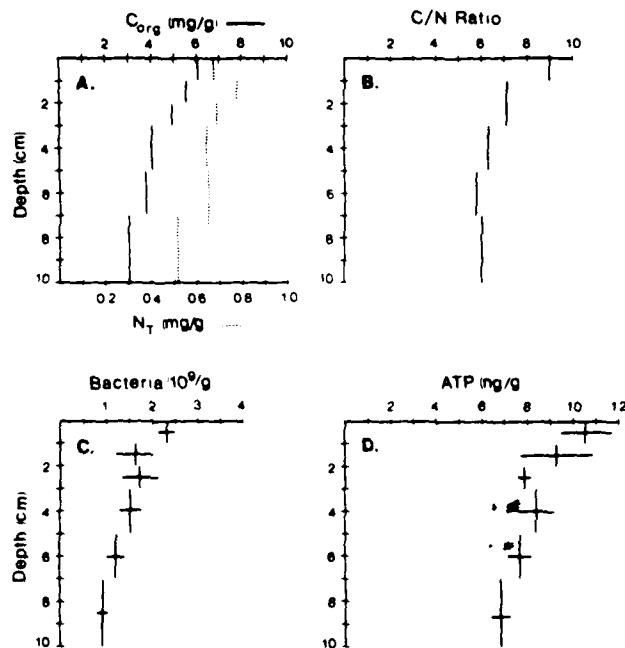


Fig. 3. Profiles of organic carbon and total nitrogen concentration (A), C/N weight ratios (B), bacterial densities (C), and ATP concentrations (D) from a box core 6 Station 14 KNORR 78 April–May 1980, HEBBLE area, Nova Scotian Rise ($40^{\circ}24.37'N$, $63^{\circ}09.52'W$) 4617 m. Values for (C) and (D) from the top 2 cm are means of two separate counts or extractions from each of 12–100 cm^2 subcores. The lower depth intervals are equal to means of two separate analyses from each of 8–100 cm^2 subcores.

organic carbon concentrations, the micro-organism distributions, and the high macro- and meiofaunal population abundances mentioned previously. Organic carbon concentrations appear to be twice as high throughout the top 10 cm as previously reported from other deep-sea regions (Fig. 3A) (Müller, 1977). The high C/N ratio relative to a plankton source indicates that the material has been subject to at least partial decomposition elsewhere. The observed decrease in carbon with depth in sediments at the HEBBLE site (Fig. 3B), on the other hand, implies that the surficial organic matter is not completely refractory and can be further metabolized. There are few deep-sea data with which to compare sediment ATP concentrations and bacterial densities, but it does appear that bacterial abundances and, by inference, microbial activity in these HEBBLE region sediments are higher than in many other deep-sea localities. The observations are consistent with the relatively abundant metabolizable carbon measured (Fig. 3C and D) (Karl et al., 1976; Norkrans and Stehn, 1978).

CONCLUSIONS

Our first examination of the deposits in the HEBBLE study area suggests a deep-sea region alternately influenced by periods of strong near-bottom currents which erode and transport sediments and periods of weaker flow when sediment reworking by a shallow burrowing (2–3 cm) benthic infauna dominates particle transport. This temporal alteration of physical and biological activity is not evident in bottom photographs (Fig. 1B) but, is preserved in the sedimentary fabric as observed in X-radiographs.

Future studies in the HEBBLE region will allow us to better understand organism–sediment–flow interactions and their impact on sediment transport, the functional structure of benthic communities, and possibly the genesis of bedforms in the deep-sea.

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REFERENCES

- Aller, R.C., 1980. Diagenetic processes near the sediment–water interface of Long Island Sound. I. Decomposition and nutrient element geochemistry (S, N, P). In: B. Saltzman (Editor), *Advances in Geophysics*. Academic Press, New York, N.Y. 22: 237–250.
- Aller, R.C. and Yingst, J.Y., 1980. Relationships between microbial distributions and the anaerobic decomposition of organic matter in surface sediments of Long Island Sound, USA. *Mar. Biol.*, 56: 29–42.

- Biscaye, P.E., Gardner, W.D., Zaneveld, R.J., Pak, H.S. and Tucholke, B.E., 1980. Nephels! Have we got nephels. *Trans. Am. Geophys. Union*, 61, p. 1014.
- Bulleid, N.C., 1978. An improved methods for the extraction of adenosine triphosphate from marine sediment and sea water. *Limnol. Oceanogr.*, 23: 174-178.
- Christian, R.R., Bancroft, K. and Wiebe, U.S., 1975. Distribution of microbial adenosine triphosphate in salt marsh sediments at Sapelo Island, Georgia. *Soil Sci.*, 119: 89-97.
- Gaudette, H.E., Flight, W.R., Toner, L. and Folger, D.W., 1974. An inexpensive titration method for the determination of organic carbon in recent sediments. *J. Sediment. Petrol.*, 44: 249-253.
- Heezen, B.C. and Hollister, C.D., 1971. *Face of the Deep*. Oxford Univ. Press, New York, N.Y., 659 pp.
- Hessler, R.R. and Jumars, P.A., 1974. Abyssal community analysis from replicate box cores in the central North Pacific. *Deep-Sea Res.*, 21: 195-209.
- Hobbie, J.E., Daley, R.J. and Jaspers, S., 1977. The use of nucleopore filters for counting bacteria by fluorescence microscopy. *Appl. Environ. Microbiol.*, 33: 1225-1228.
- Hollister, C.D. and Heezen, B.C., 1972. Geologic effects of ocean bottom currents: Western North Atlantic. In: A.L. Gordon (Editor), *Studies in Physical Oceanography*. Gordon and Breach, New York, N.Y., 2: 37-66.
- Jumars, P.A., Nowell, A.R.M. and Self, R.F.L., 1982. A simple model of flow-sediment-organism interaction. *Mar. Geol.*, 42: 155-172.
- Karl, D.M., Morse, J.W. and Sturges, W., 1976. Adenosine triphosphate in the North Atlantic Ocean and its relationship to the oxygen minimum. *Deep-Sea Res.*, 23: 81-88.
- Kerr, R.A., 1980. A new kind of storm beneath the sea. *Science*, 208: 484-486.
- Müller, P.J., 1977. C/N ratios in Pacific deep-sea sediments: Effect of inorganic ammonium and organic nitrogen compounds sorbed by clays. *Geochim. Cosmochim. Acta*, 41: 765-776.
- Norkrans, B. and Stehn, B.O., 1978. Sediment bacteria in the deep Norwegian Sea. *Mar. Biol.*, 47: 201-209.
- Nowell, A.R.M., Jumars, P.A. and Eckman, J.E., 1981. Effects of biological activity on the entrainment of marine sediments. *Mar. Geol.*, 42: 133-153.
- Rhoads, D.C. and Boyer, L.F. In press. The effects of marine benthos on physical properties of sediments; a successional perspective. In: M.J.S. Tevesz and P.L. McCall (Editors), *Animal-Sediment Relations: The Biogenic Alteration of Sediments*. Plenum Press, New York, N.Y.
- Richardson, M.J., Wimbush, M. and Mayer, L., 1981. Exceptionally strong near-bottom flows on the continental rise of Nova Scotia. *Science*, 213: 887-888.
- Tucholke, B.E., Hollister, C.D., Biscaye, P.E., Gardner, W.D. and Sullivan, L.G., 1979. *Trans. Am. Geophys. Union*, 60, p. 855.
- Tucholke, B.E., Hollister, C.D., Biscaye, P.E. and Gardner, W.D., 1980. Current produced bedforms in HEBBLE study area Nova Scotian continental rise. *Trans. Am. Geophys. Union*, 61, p. 1014.
- Watson, S.W., Novitsky, T.J., Quinby, H.L. and Valois, F.W., 1977. Determination of bacterial number and biomass in the marine environment. *Appl. Environ. Microbiol.*, 33: 940-946.

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